PHOTOSYNTHESIS, RESPIRATION, TRANSPIRATION, AND GROWTH OF *ACACIA KOA* SEEDLINGS AS AFFECTED BY PHOTOSYNTHETIC PHOTON FLUX DENSITY

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ABSTRACT

Acacia koa Gray is Hawaii's most valuable forest tree. It is considered a pioneering species because it becomes established rapidly after overstory removal if seeds are present in the soil. The two leaf forms of koa apparently allow it to gain and then maintain control of the site. Leaves and phyllodes of koa differ markedly in leaf orientation, morphology, and anatomy, and in the levels of chlorophyll, total soluble protein, and Ribulose-1,5-bisphosphate carboxylase. Both leaf forms have similar CO_2-exchange rates when determined on a leaf area basis. Mean maximum rates of photosynthesis for both leaf forms were about 24 mg CO_2 $dm^{-2}h^{-1}$. Light saturation and light compensation for both leaf forms occurred at 1200 and 25 μmol $m^{-2}s^{-1}$, respectively. The CO_2 compensation concentration was about 55 ppm for both leaves and phyllodes, indicating that both leaf forms fix CO_2 via the C_3-pathway. On an organ basis leaves have higher CO_2-exchange rates than phyllodes. Leaves also have higher transpiration rates than phyllodes.

Growth and development of koa seedlings was greatly affected by available light. Seedlings grown under the highest light levels were the tallest and had the largest stem diameter and total dry weight. All measured growth parameters decreased as light intensity decreased. As the seedlings grew and developed under the different light levels, roots as a percentage of the total dry weight remained a fairly constant 18 percent. Initially, leaves made up more than 50 percent of the total dry weight. The percentage of leaf dry weight

decreased with time, while the percentage of stem dry weight increased. Phyllodes developed only on seedlings exposed to light of at least light-saturating levels. The data indicated that koa seedlings can survive and grow only at light levels equal to or greater than 25 percent of full sunlight. The vigor of koa seedlings grown at less than 25 percent full sunlight declined with time and it appeared that they would eventually die. This minimum light requirement accounts for the scarcity of natural koa reproduction in an undisturbed koa forest.

Koa leaves and phyllodes readily adapted to changes in available light. Leaves and phyllodes grown in full sunlight developed the characteristics of sun leaves. Conversely, at 27 percent of full sunlight, both leaf forms developed the characteristics of shade leaves. Fully-developed leaves and phyllodes only adapted physiologically to changes in available light. Partially-developed leaves and phyllodes adapted both physiologically and anatomically to changes in available light.

Seedlings with phyllodes grown in 27 percent of full sunlight for 6 to 8 weeks developed leaves at the terminals. Seedlings again produced phyllodes when placed in full sunlight.

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CHAPTER I

GENERAL INTRODUCTION

Koa (Acacia koa Gray) has been called the Monarch of Hawaiian forests. This is a fitting description of this native leguminous species that occurs on all the larger islands, forming a part of the forest cover on about 500,000 acres (Nelson and Wheeler 1963), or about 25 percent of the forested areas of the state. Koa, one of the most common native tree species of the Hawaiian Island ecosystem, provides a habitat for several species of native birds (Goodwin and Aldrich 1966, Munro 1960), mollusks (Kondo 1970), and insects (Gagne et al. 1970, Gressitt and Davis 1969, Swezey 1925). Many native plant species grow in association with koa.

Koa is also a renewable economic resource and is Hawaii's most valuable timber tree. Skolmen (1970) estimated that the koa industry generates more than $1.3 million per year. Koa grows to heights of more than 45 m. The circumference of one tree measured 8.4 m (Littlecott 1969). The technical wood properties of koa are almost identical to those of black walnut (Juglans nigra L.) (Skolmen 1968) and the beauty of finished koa and black walnut are comparable. Koa has many uses, but because of its high value, it is used mainly for cabinets, furniture, gun stocks, veneer, and craft pieces.

Koa forests are not as extensive today as they once were (Hall 1904, Whitesell 1964) and the area continues to dwindle for a number of reasons. In the past 50 years, an estimated 100,000 acres of koa forest have been cleared for pasture. Koa is relished by cattle who prevent the regeneration of koa forests by eating all seedlings and

sprouts. Koa forest regeneration is also hampered by competition from numerous introduced and native plant species and by insects and diseases that attack young and old trees. Fire has also taken its toll on koa forests. One fire burned for more than 2 months through the koa forests on the island of Hawaii. Logging has not reduced the area of koa forests because koa regenerates rapidly in openings created by logging.

If koa forests are to be perpetuated at their present extent, or perhaps increased, both natural and artificial regeneration must be accomplished. Natural koa regeneration is scarce in undisturbed forests. Approximately 200 to 300 seedlings and root suckers per acre are present in an established forest and most are of recent origin. The majority of seedlings present are less than 3 inches tall; most root suckers are less than 2 feet tall. Few seedlings survive for more than 1 year (Scowcroft and Nelson 1976). However, if the forest canopy is removed and the mineral soil is exposed, seeds which may have lain in the soil for 25 years (Judd 1920), germinate rapidly. Estimates of up to 143,500 koa seedlings per acre have been tallied in a plot after removal of the forest canopy (Judd 1925). Whether the high rate of germination after the disturbance resulted from increased soil temperature or light, or to an altered soil moisture or oxygen regime, or combinations of these factors, is not known.

When natural regeneration occurs in adequate numbers after removal of the upper story vegetation, spatial distribution of seedlings is generally very uneven. Artificial regeneration is therefore necessary to ensure fully-stocked forests. Artificial

regeneration has been accomplished by direct seeding (Bryan 1929, Whitesell 1967) and with planting (Walters 1974, Walters and Horiuchi 1979).

The successful and rapid establishment of a koa forest by natural or artificial means requires much information about the effects of environmental factors on the growth of koa seedlings. The climatic requirements of koa are not well known. Koa is found at elevations ranging from about 180 m (Rock 1920) to 2100 m (Judd 1920), but reaches its greatest development in size and number at elevations of 1500 to 1800 m. The mean January temperature at these elevations is about 12° C; the mean August temperature is 15° C. Although koa occurs in semiarid to wet areas, it attains its greatest development in areas that receive 1900 to 5000 mm of rain annually (Whitesell 1964). Irradiance in the koa forest varies from full sunlight in openings, probably greater than 1350 Wm^{-2} [Photosynthetically Active Radiation (PAR) 400-700 nm] at 1500-m elevation, to perhaps less than one-tenth full sunlight under a forest canopy.

Koa seedlings are heterophyllous. They initially bear leaves that are finely divided, consisting of five to seven pairs of pinnae, each pinna with 12 to 24 pairs of leaflets. These true leaves give way to smooth, stiff crescent-shaped "leaves" which are in fact expanded petioles called phyllodes (Neal 1965, Rock 1920) (Fig. 1). During the transition from true leaves (juvenile form) to phyllodes (mature form) (Hartmann and Kester 1975), it is common to see true leaves attached to the phyllodes. Generally, mature trees bear only phyllodes. However, if the trunk is wounded, the sprouts that often

Figure 1. Acacia koa seedling with
a) leaves and b) phyllodes.

develop near the wound have true leaves (Rock 1913).

Photosynthetic photon flux density (PPFD) is one of the most important environmental factors because it supplies the energy required for plant photosynthesis, growth, and development. Photosynthetic photon flux density can be readily manipulated in the nursery and forest so that seedlings are exposed to optimum levels during ontogeny, thus promoting rapid growth and development. In the nursery, PPFD can be controlled by the use of lamps or shade cloth. In the forest, it can be controlled by manipulating species composition and spacing.

However, the present lack of data on the relationship between PPFD and photosynthesis and growth of koa, makes it impossible to develop management strategies for promoting koa growth by manipulating the light regime. This research was conducted to accomplish the following objectives:

Objective 1--Determine the photosynthetic, respiration, and transpiration characteristics of leaves and phyllodes of Acacia koa.

Objective 2--Determine the photosynthetic, respiration, and growth characteristics of Acacia koa seedlings exposed to different PPFD.

Objective 3--Determine how Acacia koa leaves and phyllodes adapt to changes in PPFD.

CHAPTER II

GENERAL LITERATURE REVIEW

Despite the economic and ecological importance of koa, data describing its growth and development in the nursery and field and the physiological biochemical data necessary to explain that growth and development, are lacking. Because 90 to 95 percent of the dry weight of plants are derived from photosynthetic CO_2 assimilation (Zelitch 1975a), an understanding of the partitioning of photosynthate into various plant parts is necessary. Some of the CO_2 fixed during photosynthesis is utilized by respiration in the light and darkness to produce energy and products that are used in the maintenance and construction of plant tissue (Ledig et al. 1976). The rate of photosynthesis is often related to water deficits in the plant. As deficits occur because moisture loss by transpiration exceeds uptake, cell elongation rates decline and eventually photosynthetic rates decrease because of increased stomatal and mesophyll diffusive resistances (Begg and Turner 1976, Zelitch 1975b).

This general literature review will focus on the processes of photosynthesis, respiration, transpiration, and their subsequent effects on plant growth and development. Because of the lack of information on Acacia species in general, and koa specifically, the review includes information on other tree and plant species.

Carbon Dioxide Exchange of Leaves

Photosynthesis is a photochemical reaction in which water plus carbon dioxide (CO_2) in the presence of light and chlorophyll yields sugar. The overall reaction of photosynthesis is given by the

simplified equation:

$$nCO_2 + 2nH_2O^* + \text{light} \xrightarrow{\text{chloroplasts}} (CH_2O)_n + nO_2^* + nH_2O$$

The initial phase of photosynthesis is the trapping of light energy by chlorophyll contained in plant organs, principally the leaves. During this phase, electrons are removed from water, oxygen is released, and high energy pyridine nuceleotide and adenosine triphosphate molecules are produced. These energy-rich molecules are used to reduce carbon dioxide during the second phase of photosynthesis as well as to provide energy for other physiological processes (Zelitch 1971). This energy-trapping process of the initial phase is apparently the same for all higher plants, but the manner in which the plant reduces carbon dioxide varies with species (Govindjee and Govindjee 1974).

All woody plants and trees examined thus far, with the exception of mangrove (Joshi et al. 1974) and larch (Fry and Phillips 1976), have characteristics of C_3 plants (Downton 1971). Classification as a C_3 plant implies the absence of a highly photosynthetically active vascular bundle sheath in the leaf tissue, the potential of high rates of photorespiration, the predominance of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPcase) as the major photosynthetic CO_2 fixation enzyme, and a minimum CO_2 compensation concentration of about 50 ppm CO_2 (Black 1973, Zelitch 1971). Photorespiration reduces net photosynthesis by releasing part of the CO_2 fixed in photosynthesis with a loss of energy associated with its fixation (Black et al. 1976, Chollet and Ogren 1975, Goldsworthy 1970, Schrader 1976, Zelitch 1975a). The high CO_2 compensation concentration

results from photorespiration. The rate of photorespiration of C_3 plants is greatest at high temperatures and PPFD and may be as high as 50 percent of net photosynthesis (Zelitch 1975b). However, under the relatively cool temperatures and moderate PPFD commonly experienced by most forest trees in temperate zones, photorespiration does not prevent trees from attaining productivities which are often as high as for plants with low photorespiration under similar conditions (Bjorkman and Berry 1973, Gifford 1974, Zelawski and Walker 1976).

The principle reaction in the reduction of carbon dioxide via the Calvin Cycle or C_3 pathway is the carboxylation and splitting of ribulose-1,5-bisphosphate (RuBP) to yield two molecules of 3-phosphoglyceric acid which in turn can be converted into sugars. The rest of the cycle is a reduction of 3-phosphoglyceric acid to triose phosphate, followed by a series of rearrangements to regenerate the RuBP (Zelitch 1971). The reduction of carbon dioxide is termed the "dark reaction" because it can occur in the absence of light.

Photosynthetic rates are often determined at the light-saturation and light-compensation points. The light-saturation point is the PPFD at which the rate of CO_2-uptake does not increase with further increases in PPFD. Plants adapted to grow in full sunlight generally have higher light-saturation rates than plants adapted to grow in shade (Boardman 1977). Bohning and Burnside (1956) determined the light-saturation rates for a representative sample of sun and shade plants. They found that the CO_2-uptake by sun species was saturated at a PPFD of 400 to 600 $\mu mol\ m^{-2}s^{-1}$, whereas shade species were saturated at 60 to 200 $\mu mol\ m^{-2}s^{-1}$. Light-saturated rates of

photosynthesis were considerably higher in the sun species (16-20 mg CO_2 $dm^{-2}h^{-1}$) than in the shade species (2-5 mg CO_2 $dm^{-2}h^{-1}$).

The light-compensation point is the PPFD at which the rate of CO_2 release is equal to CO_2-uptake at a constant CO_2 concentration and some physiological temperature. This point is a useful indicator of the maintenance requirement of plants at low PPFD (Schaedle 1975). Characteristically, shade-adapted leaves have a much lower light-compensation point than light-adapted leaves (Loach 1967, Schaedle 1975). The shade and sun species examined by Bohning and Burnside (1956) had light-compensation points of 2 and 20 µmol $m^{-2}s^{-1}$, respectively. Differences in light-compensation points are caused primarily by differences in respiration rates. When the respiration rate is low, the leaf requires less PPFD to photosynthesize rapidly enough to balance the CO_2 being lost, so the light-compensation point is also low (Salisbury and Ross 1978).

The CO_2-compensation point is the CO_2 concentration where photosynthetic fixation just balances respiratory loss. The CO_2-compensation point provides an indication of the pathway by which CO_2 is fixed in the leaf. A CO_2-compensation point between 0 to 5 ppm indicates the C-4 pathway, whereas a CO_2-compensation point between 50 to 100 ppm indicates the C-3 pathway (Singh et al. 1974).

Leaves and other structures capable of assimilating CO_2 follow a developmental progression from the time they are initiated and this progression influences the CO_2-exchange rate (CER) (Shibles 1976). Differences in CER are attributable to related morphological,

physiological, and biochemical events. The pattern of leaf development is similar for different species (Schaedle 1975). During leaf expansion, increases in photosynthetic CO_2-uptake can be related to development of internal leaf structure and stomates (Homann 1975, Isebrands and Larson 1973), a decrease in diffusion resistance (Homann 1975), synthesis of chlorophyll (Dickmann 1971b), development of physiological and structural integrity of the membrane-bound phosphorylation system of chloroplasts (Dickmann 1971b, Hernadez-Gil and Schaedle 1973), Fraction I protein synthesis, increases in RuBPcase activity (Dickmann 1971b), and a sharp decline in mitochondrial respiration (Dickmann et al. 1975).

A leaf is mature when leaf expansion ceases and leaf anatomy has essentially stabilized. Maturation does not proceed at a uniform rate throughout the leaf. The lamina tip matures first, both structurally and functionally, and maturation then proceeds basipetally, the leaf base and margins maturing last (Isebrands and Larson 1973). At maturity, mesophyll cells and intercellular spaces are fully developed, stomatal formation is complete, and the leaf vascular system is fully functional (Isebrands and Larson 1973). A leaf that has reached anatomical maturity is functionally mature as well (Dickmann et al. 1975). The potential capacity for net photosynthesis is maximum and CO_2-compensation concentration and dark respiration reach a minimum (Dickmann 1971a, Dickmann and Gjerstad 1973, Larson et al. 1969, Loach and Little 1973). The Hill reaction and RuBPcase activities are maximum (Dickmann et al. 1975, Ghosh 1973). A mature leaf functions only as an exporter of photosynthate (Larson et al.

1969), although an expanding leaf may be exporting simultaneously from mature regions and importing to immature regions (Larson et al. 1972, Schaedle 1975).

Following the completion of leaf expansion, a more or less steady state condition of photosynthetic performance persists for a duration of 10 to 40 days, depending on species, time of year, and environmental conditions (Schaedle 1975). Subsequently, with increasing leaf age, net photosynthesis declines (Bormann 1956, Bormann 1958, Clark 1961, Dickmann 1971a, Freeman 1952, Furukawa 1973, Kozlowski and Keller 1966, Logan 1970, Thrower 1967, Wardlaw 1968). Associated with this decline is a reduction in the chlorophyll, protein, and nucleic acid content of the leaf (Schaedle 1975), and diffusive resistance to water and CO_2 increase (Davis and McCree 1978).

The photosynthetic activity of the whole plant is greatly affected by the proportion and arrangement of photosynthetically active leaves. The maintenance of high photosynthetic activity is dependent on the continued adding of and the rapid maturation of leaves (Dickmann 1971b). Many tree species progress through several distinct leaf stages during their first year; cotyledons are followed by primary leaves, and eventually, secondary leaves. Each leaf type is morphologically and anatomically distinct (Ledig et al. 1976). Marshall and Kozlowski (1976) found that cotyledons of woody angiosperms contributed significantly to the plants' chances for survival and growth if care was taken to avoid injury and to provide them with favorable conditions. Primary leaves have higher rates of

CO_2-uptake than secondary leaves (Ledig et al. 1976).

The CER or net photosynthesis (mg CO_2 $dm^{-2}h^{-1}$) is the algebraic sum of CO_2 fixed photosynthetically and CO_2 released by respiration. Under near optimal conditions, trees have CER that range from 10 to 30 mg CO_2 $dm^{-2}h^{-1}$ (Brix 1967, Krueger and Ferrell 1965, Krueger and Ruth 1969, Schaedle 1975, Verduin 1953). Jarvis and Jarvis (1964) found that maximum rates of CO_2-uptake for temperate zone evergreen conifers ranged from 5 to 10 mg $CO_2 dm^{-2}h^{-1}$ compared to rates of 10 to 20 mg CO_2 $dm^{-2}h^{-1}$ for deciduous broad-leaved trees and shrubs. Larcher (1969b) reported that photosynthetic rates of evergreen broad-leaved species from temperate and warm temperate regions ranged from 14 to 17 mg CO_2 $dm^{-2}h^{-1}$. However, many values of net photosynthesis found in the literature are thought to be unreliable because of peculiarities in the method of determination (Brittain and Cameron 1973, Jarvis and Jarvis 1964). Differences in environmental factors--light intensity and quality, water, nutrition, CO_2 content--and differences in plant material--attached or detached leaves, sun leaves or shade leaves, seedlings or larger plants--used by researchers are factors which could have affected photosynthetic rates (Zelawski and Walker 1976).

Transpiration by Leaves

Transpiration is the loss of water by evaporation from plants. It differs from the general process of evaporation, because the water vapor does not evaporate from a free surface but must pass through the epidermis and cuticle or through pores; i.e., the stomata or lenticels. Transpiration may take place from any exposed part of the

plant, but the structure and position of the leaves are such that the greatest loss of water usually occurs through them. Transpiration from leaves occurs through the cuticle and the stomates. Stomatal transpiration generally represents more than 90 percent of the water lost by plants (Hill et al. 1960).

Transpiration (T) is described by the equation $T = \frac{\Delta H_2O}{r_a + r_e}$ where $\Delta H_2\Theta$ is the water vapor pressure gradient between the leaf and the air and r_a and r_e are the boundary layer and leaf resistances, respectively. The value of r_a is proportional to $L^{0.25} v^{-0.5}$ where L is leaf or leaflet area and v is wind velocity (Milthorpe and Moorby 1974). Surface roughness of the leaf also affects the boundary layer resistance. Leaf resistance is determined primarily by the stomatal resistance and the resistance of the cuticle. Stomatal resistance may vary widely as the stomates open and close. The rate of transpiration varies with species and the environment under which that species has grown and is presently growing. Representative transpiration rates for crop plants and trees are given in Table 1. The rates shown are representative but not truly comparable because the values were not obtained under the same conditions of air temperature, radiation load, humidity, wind velocity, time of day, and atmospheric pressure.

The environment affects transpiration, because of its effect upon the evaporation of water and its effect upon stomatal aperture. Increasing leaf temperature, for example, promotes evaporation, but may eventually cause stomates to close. Light causes stomates to open, but increases leaf and air temperatures. Increasing humidity

Table 1

Representative Transpiration Rates for Crop Plants and Trees

Species	Transpiration rate	Reference
	mg dm^2h^{-1}	
Tobacco (*Nicotiana tabacum* L.)	143	(Spector 1956)
Sunflower (*Helianthus annus* L.)	119	(Spector 1956)
Bean (*Phaseolus vulgaris* L.)	108	(Louwerse and Zweerde 1977)
Corn (*Zea mays* L.)	288	(Louwerse and Zweerde 1977)
Oak (*Quercus rubra* L.)	79	(Spector 1956)
Sycamore (*Platanus occidentalis* L.)	79	(Spector 1956)
Box elder (*Acer negundo* L.)	68	(Spector 1956)

decreases transpiration, but relative humidity is a function of temperature, and this in turn is influenced by light. Wind may cause an increase or decrease in transpiration. Wind increases the water vapor pressure gradient and reduces r_a by blowing away the vapor, causing an increase in evaporation. If the leaf is warmed by sunlight, wind will lower the temperature, causing a decrease in transpiration (Salisbury and Ross 1978).

Growth and Development of Plants

Growth, in terms of dry matter production, results mainly from net photosynthetic fixation of carbon dioxide (Schrader 1976, Zelitch 1975b). However, correlations between growth and photosynthesis of single leaf trees and crop plants have been weak, or even zero (Carter 1972, Elmore 1980, Gordon and Gatherum 1968, Ledig and Perry 1969, Moss and Musgrave 1971). The poor correlations result because measurements on a single leaf do not account for partitioning, for the effects of mutual shading, or for senescence of older leaves. Some of the photosynthate is utilized for maintenance respiration, as well as for growth (Baker et al. 1972, Ledig et al. 1976, McCree 1974). Maintenance respiration produces the energy to maintain tissue integrity and function. Growth respiration provides the energy and carbon skeletons for the synthesis of new tissue (Baker et al. 1972). The respiration components change with ontogeny. As plants grow, more dry weight is put in nonproductive tissues like stems and branches, whose integrity and function must be maintained. Growth respiration has been found to be proportional to photosynthesis (Ledig et al. 1976). Maintenance and growth respiration rates are substantially

higher for shoots than for roots (Ledig et al. 1976). Dry matter production per unit of soil area, often expressed as the crop growth rate ($g\ m^{-2}\ day^{-1}$), is the cumulative result of net photosynthesis by a unit area of an average leaf in the canopy multiplied by the leaf area index after deduction of photosynthate used in respiration, and thus represents accumulation of real increments of organic matter for the entire plant.

Stem growth of tree seedlings over time is usually sigmoid. During the logarithmic phase, establishment of the seedling begins as the radical penetrates the soil and the cotyledons, if they are epigeal, begin to carry on photosynthesis. Growth rate (the increase in size per unit of time) is slow during this phase, apparently because the germinating seed has fewer cells capable of growth. The growth rate continuously increases during this phase as more cells are formed. During the second or linear phase, growth continues at a constant, usually maximum rate for some time. The third phase is the senescence phase during which dry matter continues to increase, but more slowly, so the rate decreases (Salisbury and Ross 1978).

Growth of the stem and roots has been found to be episodic and alternating (Krueger and Trappe 1967). In a study with pitch pine (Pinus rigida Mill.), Ledig et al. (1976) found that for about the first 2 1/2 months, root growth was rapid while leaves were slowly increasing in dry weight. For the next 3 1/2 months, root growth was nil while leaf growth was rapid. Then the phase shifted so that root growth was again rapid. Although growth of the stem and roots alternated, the rate of dry weight gain for the whole plant was nearly

linear over the entire period of measurement.

Growth can be defined in terms of increased dimension, mass, or combinations of these for the whole plant or plant organ. For growth analysis, the primary values are usually the dry weight of whole plants and/or parts (stems, leaves, roots), and the dimensions of assimilatory apparatus (leaf area, weight of chlorophyll, etc.). These values are determined at specified intervals, and from them calculations are made that describe the growth of the plants and their various parts as well as the relationship between assimilatory apparatus, generally leaves, and dry matter production.

Relative growth rate (RGR), milligrams dry weight produced per gram of dry matter per unit of time, indicates the efficiency of dry matter production under specific environmental conditions (Brix 1967). The RGR can be calculated by multiplying the net assimilation rate (NAR) by the leaf area ratio (LAR). The NAR describes the net production efficiency of the assimilatory apparatus and can be calculated using one of several formulas. The formula used in this study was:

$$NAR = \frac{W_2 - W_1}{A_2 - A_1} \cdot \frac{\ln A_2 - \ln A_1}{t_2 - t_1}$$

where W_2 and W_1 are the total plant dry weight at initiation (t_1) and at some later time (t_2), A_2 and A_1 are the total projected plant leaf area at times t_1 and t_2 and $t_2 - t_1$ is the sampling interval.

This formula assumes that A and W are linearly related.

Leaf area ratio (LAR) is defined as the ratio between projected leaf area and total dry weight for an average plant and indicates the amount of leaf area displayed per gram of dry matter.

Jarvis and Jarvis (1964) calculated the RGR and NAR for 12 broad-leaved and four coniferous tree species. The RGR of dicotyledonous broad-leaved woody trees averaged about 172 mg g^{-1} wk^{-1} and ranged from 53 to 300 mg g^{-1} wk^{-1}. The RGR of coniferous trees averaged only 95 mg g^{-1} wk^{-1} and ranged from 23 to 229 mg g^{-1} wk^{-1}. Net assimilation rates of broad-leaved species averaged 30 g m^{-2} wk^{-1} and ranged 13 to 69 g m^{-2} wk^{-1}; coniferous species averaged 26 g m^{-2} wk^{-1} and ranged from 11 to 42 g m^{-2} wk^{-1}.

Helms (1970) reported that a natural, all-age-stand (1 to 75 years) of ponderosa pine (Pinus ponderosa Laws.) had an NAR of 157 g m^{-2} wk^{-1} during the summer months, which surpasses all the herbaceous species listed by Jarvis and Jarvis (1964). On an annual basis, tropical rain forests have even higher rates (Jordon 1971).

CHAPTER III

PHOTOSYNTHESIS, RESPIRATION, AND TRANSPIRATION OF JUVENILE AND MATURE LEAF FORMS OF *ACACIA KOA*

Introduction

Koa, like other species in the genus *Acacia*, is heterophyllous (Pedley 1975). Thus, a determination of the photosynthetic, respiration, and transpiration characteristics of koa (*Acacia koa*) requires that the two leaf forms common to koa be studied. The bipinnately compound juvenile leaves are the first true leaves to develop on seedlings. These horizontally-displayed leaves are later replaced by vertically-displayed mature leaves or phyllodes. The phyllode is an expanded petiole which forms a simple leaf. The development of phyllodes is initiated by aging and by changes in levels of light and temperature. It has been reported that phyllodes are more stress tolerant than juvenile leaves. The effect of leaf type on dry matter accumulation is not known.

This study was made to determine the photosynthetic, respiration, and transpiration characteristics of leaves and phyllodes of koa. The photosynthetic characteristics included were net photosythetic rates at different PPFD, light-saturation and light-compensation levels, and CO_2 compensation levels. The morphological and anatomical characteristics of leaves and phyllodes were determined, as were their levels of chlorophyll and RuBPcase.

Literature Review

Some species of *Acacia* develop phyllodes within weeks after germination. Unlike *Acacia mangium* Willd. and *A. harpophylla* F.

Muell., A. koa does not develop phyllodes until some months after germination. The development of phyllodes by koa is associated with increasing physiological age and a reduced rate of shoot growth. For example, formation of phyllodes is initiated on slow-growing lateral shoots at a time when the rapidly-growing terminal leader is still forming juvenile compound leaves. Reversion from adult to juvenile foliage occurs if slow-growing shoots are forced into rapid growth by environmental manipulation such as increased supplies of water or fertilizer (Borchert 1976). Genetic variability of heterophylla development in seedling populations of A. melanoxylon R. Br. has been shown by Borchert (1976). The shoot elongation rate of some plants was less than one-half the average rate and phyllodes formed very early on these plants while others grew rapidly and retained juvenile leaves for a long time.

The modification of phenotype that occurs with the conversion from leaves to phyllodes is an apparent adaption to increased temperature and aridity (Allsop 1965, Coaldrake 1971). The relative size of the bipinnate leaves of A. melanoxylon and the rate of change from leaves to phyllodes were related by Farrell and Ashton (1978) to site rainfall. Leaves were larger and were retained longer on seedlings growing on sheltered sites than on seedlings growing on exposed sites. Phyllode shape and size of A. melanoxylon were highly correlated with the distribution of annual rainfall. Phyllodes in drier areas were smaller and more symmetric than phyllodes in wetter areas (Farrell and Ashton 1978).

Leaves and phyllodes of Acacia species are inclined (measured

from the horizontal) at different angles. Leaves are displayed horizontally. Phyllodes are displayed almost vertically. The mean phyllode inclination for A. harpophylla was 83° (Connor, et al. 1971). Leaf inclination influences irradiance penetration through the leaf canopy, and therefore determines the energy available to leaves and/or phyllodes for photosynthesis. The greater the leaf inclination, the smaller will be the direct irradiance, therefore, steeply-inclined leaves have lower CER than horizontal leaves. However, a canopy of steeply-inclined leaves can have a greater CER than an equivalent canopy having horizontal leaves (Trenbath and Angus 1975). The higher rate is due to enhanced efficiency of light utilization.

The effect of leaf inclination on CER is strongly related to and interacts with leaf area index (LAI) and PPFD level (Gordon and Promnitz 1976, Loomis and Williams 1969, Saeki 1960). As LAI increases, more self and mutual shading occurs. Shading alters the photosynthetic light response characteristics of individual leaves. Shaded leaves have lower light-saturation and light-compensation points than do nonshaded leaves. The more LAI increases and PPFD level decreases, the more important it becomes to have steeply-inclined leaves if maximum photosynthetic rates are to be sustained.

The effects of self and mutual shading can be reduced by increasing the PPFD so that light penetrates the canopy and reaches the interior and lower leaves (Hughes 1969). Under such conditions, light above the first layer of leaves exceeds that required to

saturate photosynthesis, and light within the canopy may approach saturation. Therefore, the greater the extent of mutual shading the higher the light intensity required for maximum photosynthetic rates (Kramer and Decker 1944). Zelawski et al. (1973), using high intensity diffuse light that penetrated the seedling canopy from all sides, increased-light saturation values of the seedlings. On cloudy or overcast days, when diffuse sky-source radiation is great, total canopy photosynthesis may be greater for some species with low photosynthetic capacity than on clear days (Allen et al. 1974).

Leaf inclination also affects daily photosynthetic patterns. The rate of photosynthesis of horizontally-displayed leaves increases as the sun rises to the zenith and decreases as the sun moves toward the horizon. Because of the near vertical display of phyllodes, their daily photosynthetic pattern is characterized by a decrease as the sun rises to the zenith and an increase as the sun moves away from the zenith (Connor et al. 1971).

Photosynthetic rates have been measured only for phyllodes of the heterophyllic tree A. harpophylla (Connor et al. 1971, Tunstall and Connor 1975). I could find no data for true leaves of such trees. Under optimum conditions of moisture and temperature, the photosynthetic rate of naturally-displayed phyllodes exposed to 1500 $\mu E\ m^{-2}s^{-1}$ light from above was 13.6 mg $CO_2\ dm^{-2}h^{-1}$. It was not stated whether the calculations were based on the projected leaf area or the total leaf area.

No literature was found to indicate morphological, anatomical, chlorophyll, or RuBPcase characteristics of juvenile leaves or

phyllodes for any Acacia species.

Materials and Methods

Establishment and Growth of Seedlings

Seed was collected from several mature trees growing at 1600-m elevation on Mount Hualalai, island of Hawaii. Seedlings for this study were grown in the greenhouse at the University of Hawaii Experiment Farm in Waimanalo, island of Oahu. The study began November 1, 1980 and was completed April 30, 1981. The solar radiation, rainfall, and temperatures for the study period are given in Appendix A. The solar radiation inside the greenhouse was about 70 percent of that outside as determined with a Lambda Instruments Inc. LI-190 quantum sensor. Temperatures inside the greenhouse averaged 5^{o} C above the outside temperatures.

The seed was screened for size and placed in boiling water that had just been removed from the heat source, and let stand for about 4 hours. One imbibed seed was sown into each plastic pot. The pots were 15 cm wide by 18 cm deep. The rooting medium was peat moss and vermiculite, 1 to 1 by volume. No Rhizobium bacteria was added to the media because nodules developed naturally on koa roots during earlier studies. The pots were placed in the greenhouse under 55 percent shade. Irrigation was sufficient to keep the rooting medium moist. About 6 g of Osmocote fertilizer (14-14-14) was placed on the surface of the growing media in each pot. Emergence began 4 days after sowing and was complete 3 days later. When the seedlings were about 15 cm tall, the shade was removed.

When the seedlings were 3 months old, six seedlings having

similar morphological and anatomical characteristics were selected for leaf characteristic, gas exchange, chlorophyll, total soluble protein, and Ribulose-1,5-bisphosphate carboxylase determinations. These same determinations were made on phyllodes of six seedlings when they were 5 months old.

Leaf Characteristic Determination

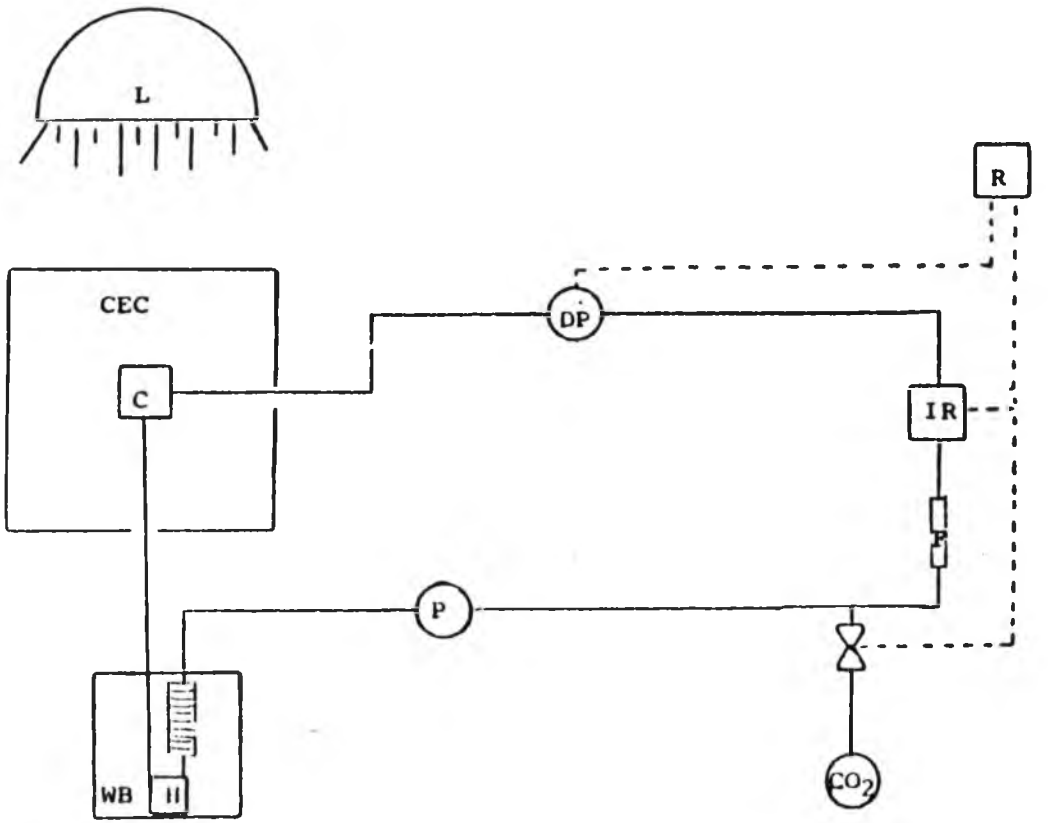
The fourth fully-expanded leaf and phyllode, representing Leaf Plastochron Index 4 (LPI-4) (Larson and Isebrands 1971), were used. The uppermost leaf or phyllode that had expanded at least 4 cm was used as the index leaf (LPI-0). The next oldest leaf below the index leaf was LPI-1, the second oldest leaf LPI-2 and so on down the stem. An ontogenetic series is thereby formed, which defines at any given time the development stage of each leaf and relates leaves at comparable morphological stages (same LPI) on different plants. If leaf or phyllode LPI-4 could not be used because of insect or mechanical damage, leaf or phyllode LPI-5 was used instead. Leaf length and width at the point of maximum dimension were measured. Leaf surface was classified as glabrous, pubescent, or other. The number of stomates per square millimeter and their size were determined by microscopic observation. Leaf thickness was determined using a dial-micrometer. Specific leaf weight was determined on a fresh and dry weight basis by dividing fresh weight and dry weight, respectively, by leaf area. Leaf area was determined using a Lambda Instruments Inc. LI-3000 area meter.

Gas Exchange Determinations

The CER, dark respiration, CO_2-compensation concentration, and

transpiration, were determined for a leaf and a phyllode on each of six different plants. Well-watered plants were placed in a growth chamber. The growth chamber environment was maintained at 70 ± 5 percent relative humidity, 26 ± 2° C temperature, and 1200 µmol $m^{-2}s^{-1}$ PPFD, using a Lucalox high pressure mercury vapor lamp. The diffuse light was filtered through about 2 cm of water to reduce infrared radiation. The PPFD was modified by placing neutral density screens between the light source and the leaf assimilation chamber. An intact leaf or phyllode was sealed in a water-jacketed plexiglass leaf assimilation chamber which was connected in series to a Beckman IR 215 infrared gas analyzer (IRGA) and a CO_2 supply in a semi-closed system mode (Šesták et al. 1971) (Fig. 2). Temperature was maintained at 27 ± 1° C by circulating water from a constant temperature bath through the water jacket. Air and leaf temperatures within the leaf and growth chamber were monitored with 0.25 and 0.13 mm copper-constantin thermocuples, respectively. The thermocouple used to monitor leaf temperature was attached to the abaxial side of the leaf. For leaves and phyllodes in the horizontal position, the incident PPFD on the leaf within the leaf chamber was determined by holding horizontally a Lambda Instruments Inc. LI-190 quantum sensor. For phyllodes in the vertical position, the incident PPFD was determined by holding the quantum sensor vertically and doubling the reading. The air was circulated within the leaf chamber by a small fan. Changes in carbon dioxide (CO_2) and water vapor content of the air after passage over the leaves were determined using the IRGA and a General Eastern 1100 AP dew point hygrometer (Figs. 3

Figure 2. An Acacia koa phyllode in the leaf assimilation chamber for gas exchange determinations.



CEC - - -controlled environment chamber
C - - - -assimilation chamber
L - - - -light source
DP- - - -dew point hygrometer
R - - - -recorder

H - - -humidity control
WB- - -water bath
IR- - - -infrared gas analyzer
F - - - -flow meter
P - - - -pump

Figure 3. Diagram of the semi-closed system for leaf gas exchange determinations, Department of Agronomy and Soil Science.

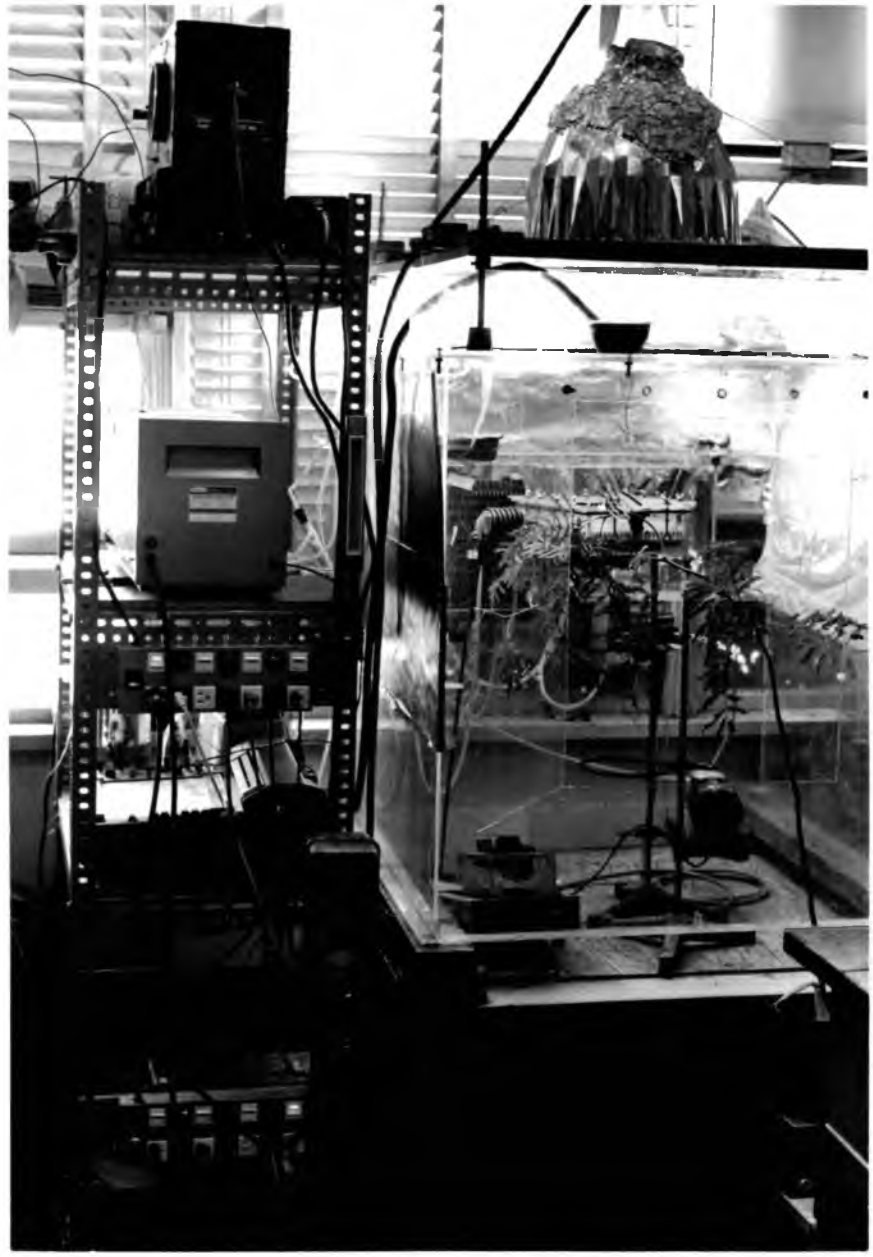


Figure 4. Semi-closed system for leaf gas exchange determinations, Department of Agronomy and Soil Science.

and 4). As the CO_2 in the air was removed by the leaf to about 290 ppm, additional CO_2 was injected into the system to bring the concentration to 320 ppm. The CO_2-uptake rate was obtained from the slope of the chart trace of the CO_2 concentration over time. Air leaving the leaf chamber was passed through a condensing coil in a constant temperature water bath to remove water vapor, thus establishing a constant dew point for the air entering the IRGA and leaf chamber. Airflow through the semi-closed system was about 1 ℓ/minute.

The CER at different PPFDs was determined by enclosing the leaf (phyllode) inside the leaf chamber and modifying PPFD. At each PPFD, the leaf was equilibrated until a steady rate of CO_2-uptake occurred before the CER was determined. The PPFD was then reduced and the CER was again determined. The CER was determined at PPFDs of 1200, 1000, 375, and 165 μmol $m^{-2}s^{-1}$ for each leaf.

Dark respiration was measured at the end of the photosynthetic measurements by turning off the light and placing a black cloth over the leaf chamber. The rate was calculated from the slope of the chart trace of the CO_2 concentration of the air leaving the leaf chamber as it increased with time over a period of about 30 minutes.

The CO_2-compensation concentration was determined by scrubbing CO_2 from the air in the system with soda lime, then allowing the leaf to replenish CO_2 until an equilibrium occurred between CO_2-uptake by photosynthesis and CO_2 release by respiration. The PPFD used for this determination was about 1100 μmol $m^{-2}s^{-1}$.

Transpiration (T) rate was calculated by the equation

$$T = \frac{(C_o - C_i)F}{A} \qquad 1$$

where C_o and C_i equal the water vapor density of the outgoing and incoming air streams (gcm^{-3}),

F equals the flow rate ($cm^3 s^{-1}$), and

A equals the projected leaf area (cm^2).

The water vapor density of the air streams was calculated from the dew point temperature of the air streams measured with a dew point hygrometer and from air and leaf temperatures. Total diffusion resistance in the leaf was calculated by the equation

$$R = \frac{C_c - [(C_o + C_i)/2]}{T} \qquad 2$$

where C_c equals the saturation water vapor density in the leaf (gcm^{-3}) at the leaf temperature and the other parameters are as given in equation 1. Leaf conductance was calculated as the reciprocal of R.

Chlorophyll Determination

The amounts of chlorophyll (chl) a, b, total chl (a + b), and their ratio (a/b) were determined using the methodology of Arnon (1949). One-half gram fresh weight of leaf material taken from the middle part of the leaf or phyllode, was ground for 15 seconds with a Brinkman Polytron homogenizer in about 15 ml of 80 percent acetone and about 0.1 g of magnesium carbonate. Magnesium carbonate was added to prevent chlorophyll breakdown. The leaf material was further extracted with acetone until colorless and the extract was filtered through Whatman No. 1 filter paper to remove plant debris. The

extract was brought to 100 ml with acetone.

Optical densities of the extracts were measured in a Beckman Spectronic 100 at wavelengths of 663 and 645 nm. The chlorophyll content of the extract was determined from a nomogram of optical density vs milligrams chlorophyll (Šestak 1971).

Total Soluble Protein and Ribulose-1,5-bisphosphate Carboxylase (RuBPcase) Determinations

Koa leaves and phyllodes were destemmed and the surface areas of 1.0-g samples were determined. The leaf sample was ground in a Brinkman Polytron homogenizer for about 10 seconds with 20 ml of an extraction solution consisting of 50 mM Tris buffer, 10 mM $MgCl_2$, and 0.2 mM EDTA, adjusted to pH 7.2 with HCl (Blenkinsop and Dale 1974). The pH of the resulting suspension was adjusted to 7.0 with NH_4OH. The suspension was centrifuged for 30 minutes at 7500 g.

The TSP content was assayed according to the method of Bradford (1976). A 0.025-ml sample was mixed with 5 ml dye-reagent solution (1 ml Bio-Rad protein assay dye reagent concentrate + 4 ml extraction solution). After about 10 minutes, the optical density of the sample was determined in a Bausch and Lomb Spectronic 20 (A_{595}). The weight of protein in the sample was determined from a calibration curve made using different amounts of bovine serum albumin in the dye reagent.

The RuBPcase content of the supernate was determined by ammonium sulfate fractionation (Paulsen and Lane 1966, Wilson and McCalla 1968) and dye-reagent techniques (Bradford 1976). The initial extract was brought to 50 percent saturation with solid ammonium sulfate (320 g/ℓ

of extract). After standing for 30 minutes, the solution was centrifuged at 13,000 g for 30 minutes. The precipitate was resuspended in 2 ml of extraction solution. A 0.012-ml sample was mixed in 5-ml dye-reagent solution (1 ml dye-reagent concentrate + 4 ml extraction solution). After about 10 minutes, the optical density of the sample was determined in a Bausch and Lomb Spectronic 20 (A_{595}). The µg of RuBPcase was determined from the same calibration curve as was used for TSP.

Data Analysis

The means and standard deviations were determined for each morphological characteristic, CER, chl a and b, TSP, RuBPcase, transpiration, and total leaf conductance for leaves and phyllodes. The degrees of freedom used in the Student's t-test for comparing the different means from samples of equal size were 18 for the morphological characteristics and 10 for all others. Unless otherwise noted, all differences reported as significant, are significant at least at the 0.05 level of probability.

Results

Morphological Characteristics

Leaves and phyllodes differed in all observed morphological characteristics. Leaves are displayed horizontally. If the rachis bends down, the leaflets adjust so their display remain horizontal. Phyllodes are displayed vertically. Average length and width of the leaves are greater than that of the phyllodes (Table 2). Average area of the leaves (one side) is almost 3 times greater than the area of phyllodes. Phyllodes, however, are more than twice as thick as the

Table 2

Morphological Characteristics of Leaves and Phyllodes of Acacia Koa

Leaf form	Length	Width	Leaf area (one side)	Thickness	Specific leaf weight	
	mm	mm	dm^2	mm	g dm^{-2} fwt	g dm^{-2} dwt
Leaves	184a+	122a	1.20a	0.23a	1.93a	0.48a
Phyllode	160b	24b	0.42b	0.48b	3.24b	0.78b

+Each value is a mean of nine observations. Values in columns followed by the same letter do not differ significantly at the 0.05 level of probability.

leaflets on leaves. Specific leaf weight of the phyllodes was about 1.7 times as great as leaves on a fresh weight basis and 1.6 times greater than that of leaves on a dry weight basis.

Anatomical Characteristics

The cross sections of koa leaflets and phyllodes are radically different (Fig. 5). Leaflets have an upper and lower epidermis, palisade layer, and spongy mesophyll. The phyllodes have two palisade layers, one on each side of the spongy mesophyll.

Leaflets and phyllodes differ in surface characteristics. Leaflets are smooth and glabrous. Phyllodes are rough because of veins which run their length. Initially, phyllodes have pubescence on both surfaces. As the phyllodes expand to full size, both epidermis become glabrous.

Phyllodes are isolateral, therefore, they have about the same stomatal frequency on both surfaces (Table 3). Leaflets are

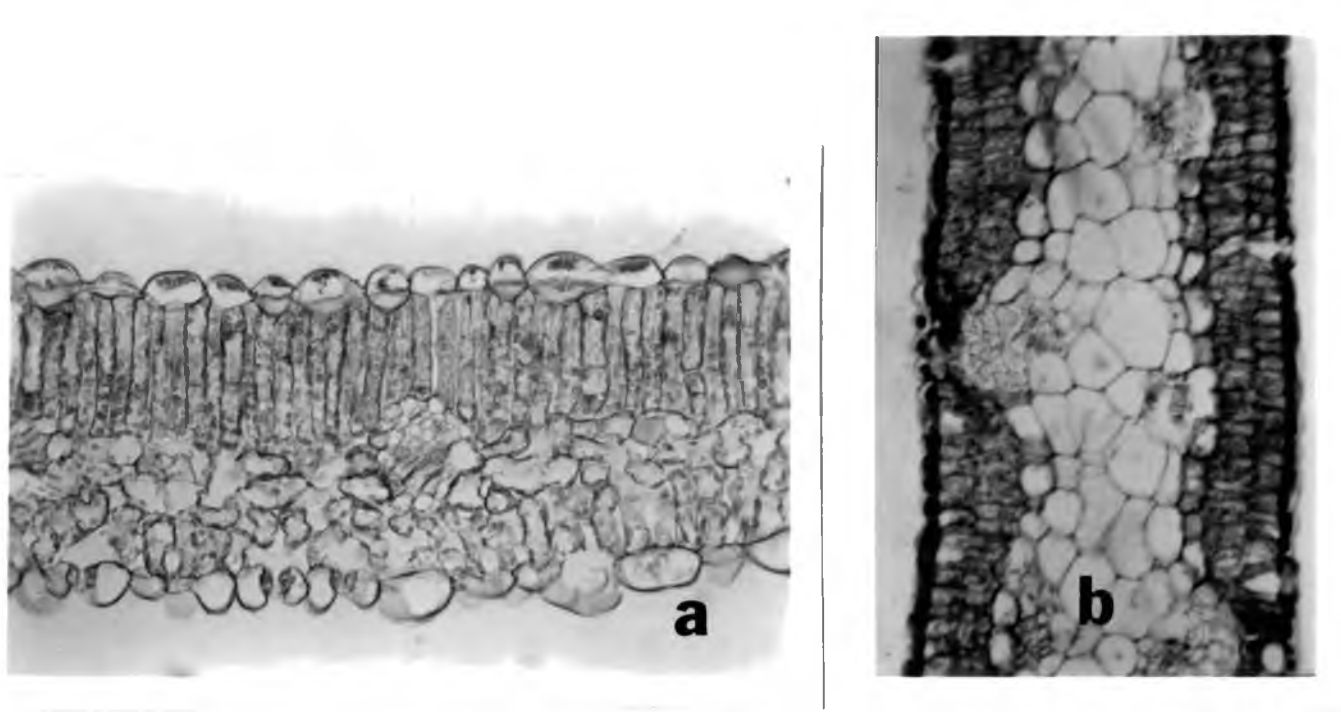


Figure 5. Cross section of a) leaflet (210X) and b) phyllode (105X) of Acacia koa.

Table 3

Stomatal Frequency and Pore Length in
Acacia Koa Leaves and Phyllodes

Leaf	Stomatal frequency: Upper (left) Epidermis	Stomatal frequency: Lower (right) Epidermis	Pore length
	- - - - mm^{-2} - - - -		mm
Leaves	+	200	.020
Phyllodes	230	230	.018

+Stomata are found only close to the major veins.

anisolateral, having greater stomatal frequency on the abaxial surface than on the adaxial surface. Leaflets have about 200 stomates per square millimeter on the lower surface and just a few stomates along the major veins on the upper surface. Average stomate pore length of the leaflet and the phyllode was similar. The total stomatal pore area per square millimeter of leaf surface (1 side of leaflets and 2 sides of phyllodes) was estimated to be 0.117 mm^2 for phyllodes compared to 0.063 mm^2 for leaflets.

CO_2-exchange Rates of Leaves and Phyllodes

Leaves and phyllodes have similar CER at a given PPFD when calculations were based on the projected unit leaf area (Fig. 6). Light saturation occurs for both leaf forms at about 1200 µmol $m^{-2}s^{-1}$ (about 60 percent of full sunlight). Mean maximum rates of photosynthesis were about 24 mg CO_2 $dm^{-2}h^{-1}$ (15 µmol m^{-2} s^{-1}) for both leaves and phyllodes. The photosynthetic rates declined with

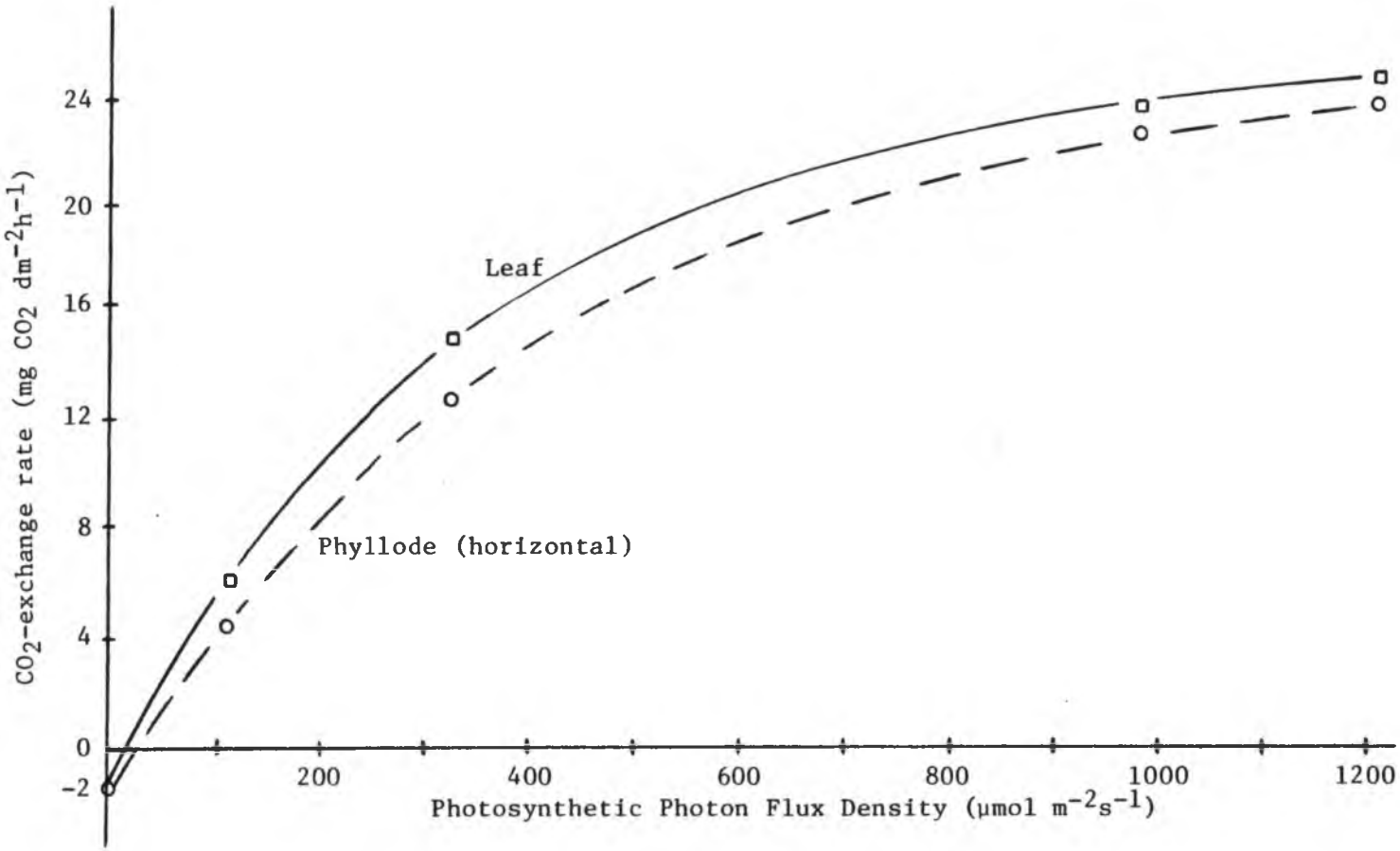


Figure 6. Rate of CO_2-exchange as a function of incident photosynthetic photon flux density of leaves and phyllodes of Acacia koa.

decreasing PPFD at about the same rate for both leaf forms. The light compensation point was about 25 μmol $m^{-2}s^{-1}$ and was similar for both leaves and phyllodes. The CO_2 compensation concentration was about 55 ppm for both leaves and phyllodes.

Although the leaves and phyllodes had similar CER when determined on a projected unit leaf area basis, they had different CER when determined on the projected organ area basis. Leaves displayed about 3 times more projected surface area than phyllodes so that on an organ basis, the CER for leaves was greater than for phyllodes (Table 4).

Table 4

CO_2-exchange Rate by a Single Fully-expanded Acacia koa Leaf and Phyllode, Based on Projected Leaf Area

Leaf form	CER at measurement PPFD (μmol $m^{-2}s^{-1}$)				
	1200	1000	375	165	Dark
	mg CO_2 $leaf^{-1}h^{-1}$				
Leaves	28.9[+]	28.2	17.8	7.2	-2.2
Phyllodes	9.6	9.3	5.4	1.8	-0.9

[+]Each value is a mean of six observations.

At PPFD of 1200, 1000, and 375 μmol $m^{-2}s^{-1}$ the CER of leaves was about 3 times that of phyllodes. At 165 μmol $m^{-2}s^{-1}$ the CER of leaves was 4 times that of phyllodes, while in the dark the difference was about 2.4 times.

Phyllodes are displayed vertically, so in nature the PPFD is

approximately equal on each side. When a phyllode was displayed vertically in the leaf chamber at a PPFD of 1200 μmol $m^{-2}s^{-1}$, the sum of the PPFD on each side of the phyllode was about 52 percent of that received on a horizontal surface. In the leaf chamber, as the PPFD was decreased by neutral shades, the sum of the PPFD on a vertical phyllode declined more rapidly than that incident on a horizontal phyllode. At a PPFD of 325 μmol $m^{-2}s^{-1}$ on a horizontal surface, the total PPFD on a vertical phyllode was about 40 percent of that on the horizontal surface and at about 125 μmol $m^{-2}s^{-1}$ on a horizontal surface, the total PPFD on a vertical phyllode was 36 percent of the incident PPFD.

CO_2-exchange rates as a function of total incident PPFD were similar for phyllodes displayed vertically and horizontally (Fig. 7). Between the light-compensation point and a PPFD of about 600 μmol $m^{-2}s^{-1}$, CERs were somewhat higher for phyllodes displayed vertically than for phyllodes displayed horizontally. The differences, however, were not statistically significant. No data were collected for vertically-oriented phyllodes at a PPFD greater than about 630 μmol $m^{-2}s^{-1}$.

Chlorophyll in Leaves and Phyllodes

Leaves and phyllodes differed significantly (0.01 level) in the amount of chl a, b and total (a + b) that they contained (Table 5). On a fresh weight basis, leaves contained about 50 percent more chlorophyll (a, b, and total) than phyllodes. On an area basis, the difference between the two leaf forms was even greater as leaves contained about 85 percent more chlorophyll than phyllodes. The ratio

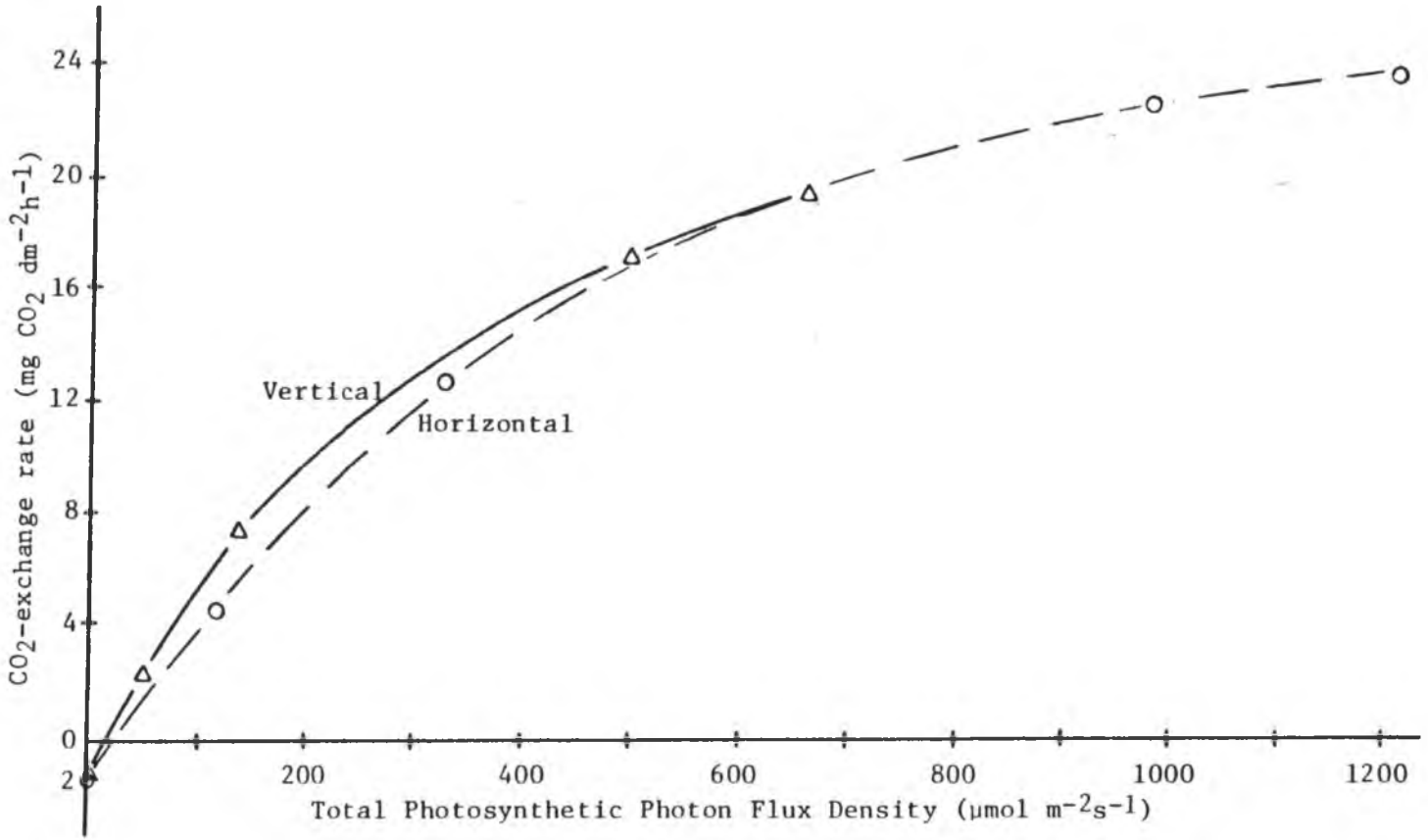


Figure 7. Rate of CO_2-exchange as a function of incident photosynthetic photon flux density of Acacia koa phyllodes in vertical and horizontal positions.

Table 5

Chlorophyll in Leaves and Phyllodes of Acacia Koa

Leaf form	Chlorophyll a		Chlorophyll b		Total (a + b)		a/b
	mg g^{-1}+	mg dm^{-2}	mg g^{-1}	mg dm^{-2}	mg g^{-1}	mg dm^{-2}	
Leaves	1.27a++	5.39a	0.47a	2.01a	1.74a	7.40a	2.7
Phyllodes	0.86b	3.01b	0.30b	1.05b	1.16b	4.06b	2.9

+Chlorophyll is expressed on a fresh weight basis.

++Each value is a mean of six observations. Values in columns followed by the same letter do not differ significantly at the 0.05 level of probability.

of chl a to b averaged about 2.7 for leaves, not significantly less than the average of 2.9 for phyllodes.

Total Soluble Protein and RuBPcase in Leaves and Phyllodes

On a fresh weight basis and on an area basis, leaves also had significantly greater amounts of TSP than phyllodes (Table 6). On a weight basis, leaves contained about 8.5 times more protein than the phyllodes. Total soluble protein made up about 18 percent of the dry weight of leaves and about 2 percent of phyllodes. On an area basis, leaves contained about 4 times more soluble protein than the phyllodes. Ribulose-1,5-diphosphate carboxylase (RuBPcase) levels of leaves on a fresh weight basis were about 12 times greater than those of the phyllodes (Table 6). On an area basis, leaves contained about 6 times more enzyme than the phyllodes.

The percentage of the total protein complex made up of RuBPcase

Table 6

Total Soluble Protein and RuBPcase+ in Leaves and Phyllodes of Acacia Koa

Leaf form	Total soluble protein		RuBPcase+	
	mg g^{-1}++	mg dm^{-2}	mg g^{-1}	mg dm^{-2}
Leaves	43.08a+++	66.34a	19.15a	29.49a
Phyllode	5.33b	17.26b	1.51b	5.13b

+Ribulose-1,5-bisphosphate carboxylase.

++Soluble protein and RuBPcase are expressed on a fresh weight basis.

+++Each value is a mean of six observations. Values in columns followed by the same letter do not differ significantly at the 0.05 level of probability.

also varies markedly between leaves and phyllodes. In leaves, about 44 percent of the TSP was represented by RuBPcase, whether calculated on a fresh weight or an area basis. In phyllodes, about 28 percent of the TSP was RuBPcase, regardless of the basis used for the calculation.

Transpiration Rate and Total Leaf Conductance of Leaves and Phyllodes

If transpiration rates are expressed on a projected unit area basis, phyllodes have significantly higher rates at 1200 and 165 µmol $m^{-2}s^{-1}$ than do leaves (Table 7). However, if transpiration rates are expressed on a projected organ area basis, leaves have rates 1.5 times greater than phyllodes at 1200 µmol $m^{-2}s^{-1}$ and 2 times greater at 165 µmol $m^{-2}s^{-1}$. In the dark, transpiration rate on a projected unit area basis is about the same for leaves and phyllodes, but on a projected organ area basis transpiration rate of leaves is twice that of phyllodes.

Table 7

Transpiration by a Single Fully-expanded Acacia koa Leaf and Phyllode, Based on Projected Unit and Organ Area

Leaf form	1200		165		Dark	
	Unit area	Organ area	Unit area	Organ area	Unit area	Organ area
	mg $dm^{-2}h^{-1}$	mg h^{-1}	mg $dm^{-2}h^{-1}$	mg h^{-1}	mg $dm^{-2}h^{-1}$	mg h^{-1}
Leaves	49.7a++	59.6	39.6a	47.5	19.1a	22.9
Phyllodes+	90.4b	38.0	56.5b	23.7	24.8a	10.4

+Phyllodes were oriented horizontally rather than in the natural vertical position.

++Each value is a mean of six observations. Values in a column followed by the same letter do not differ significantly at the 0.05 level of probability.

In the light, the mean total leaf conductance for leaves was greater than for phyllodes, but the differences were not statistically significant (Table 8).

Discussion

Photosynthetic Characteristics of Leaves and Phyllodes

A rate of CO_2-exchange at saturating PPFD for leaves and phyllodes of about 24 mg CO_2 $dm^{-2}h^{-1}$ is similar to the rates reported for eucalyptus (Brittain and Cameron 1973), apple (Malus sp.) (Heinicke and Hoffman 1933, Mika and Antoszewski 1972) and aspen (Populus sp.) (Okafo and Hanover 1978). The mean maximum CER obtained for A. koa phyllodes was about twice the rate of 13.4 mg CO_2 $dm^{-2}h^{-1}$ found for phyllodes of A. harpophylla (Connor et al. 1971, Tunstall and Connor 1975). No CO_2-exchange rates were found for leaves of

Table 8

Total Leaf Conductance of a Single Fully-expanded Acacia koa Leaf and Phyllode Based on Projected Leaf Area

Leaf form	Measurement PPFD (μmol $m^{-2}s^{-1}$)		
	1200	165	Dark
	Total conductance		
	- - - - - - cm s^{-1} - - - - - -		
Leaves	0.51a++	0.38a	0.07a
Phyllodes+	0.46a	0.29a	0.07a

+Phyllodes were orientated horizontally rather than in the natural vertical position.

++Each value is a mean of six observations. Values in columns followed by the same letter do not differ significantly at the 0.05 level of probability.

any Acacia species, probably because leaves are generally present for such a short time before being replaced by phyllodes.

The similarities of photosynthetic characteristics per projected unit area for leaves and phyllodes, including CER at saturating PPFD, efficiency of conversion of incident PPFD, and light compensation points were unexpected because the levels of chlorophyll and RuBPcase in leaves and phyllodes differed greatly. Also, the differences in organ orientation and in morphology and anatomy were great.

The absorption of PPFD depends on the overall quantity of chlorophyll, the location of chlorophyll within the leaves and phyllodes, and the ratio of chl a/b (Boardman 1977, Salisbury and Ross 1978). Although leaves have significantly more chlorophyll than phyllodes (Table 5), both leaf forms have chlorophyll levels typical of those found for other sun species (Boardman 1977, Goodchild et al. 1972). Leaves and phyllodes have most of their chlorophyll in the

palisade layers, with some found in the guard cells in the epidermis. Leaves have chlorophyll in the single palisade layer (Fig. 5) and in the guard cells of the lower epidermis (Table 3). Phyllodes have chlorophyll in both palisade layers and in guard cells in both epidermises. On a leaf area basis, only one-half the chlorophyll is on a light-absorbing phyllode surface, while all of the leaf chlorophyll is on the light-absorbing surface. When a horizontally-displayed phyllode is irradiated from above, the light penetrates sufficiently to be absorbed by chloroplasts on the opposite side as indicated by the similar CER values obtained for phyllodes orientated horizontally and vertically (Fig. 7). When the phyllode is oriented vertically as it is in nature, and illuminated from above, PPFD is absorbed by chloroplasts on both sides and light saturation is unlikely because the PPFD on one surface is about 25 percent of the direct overhead PPFD. Although phyllodes have about 55 percent of the total chlorophyll in leaves, when CER of leaves and phyllodes are expressed on a milligram of chlorophyll per dm^2 of leaf basis, the rate for phyllodes is about 72 percent greater than for leaves (Table 9). The rates of CO_2-exchange per milligram of chlorophyll for both leaves and phyllodes are similar to those reported by Kriedeman et al. (1964) for Eucalyptus regans F. Muell., Beta vulgaris L., Triticum vulgare L., and Glycine max L. Leaves and phyllodes have about the same chl a/b ratio which indicates that they depend on about the same wavelengths for photosynthesis.

Ribulose-1,5-diphosphate carboxylase (RuBPcase) is the principal enzyme in leaves and phyllodes involved in the fixation of CO_2 into

carbohydrates. The quantity of RuBPcase in a leaf varies depending on the PPFD level to which the leaf is exposed. Leaves exposed to high PPFD levels generally have more RuBPcase than leaves exposed to low PPFD (Bjorkman 1968, Boardman 1977). Acacia koa leaves are adapted to full sunlight. In fact, leaflets adjust to maintain an angle perpendicular to the sun. Because of the vertical display, koa phyllodes are not subjected to the high PPFD that leaves are. The amount of RuBPcase in leaves was 6 to 12 times greater than the amount in phyllodes, depending on whether the quantity was figured on an area or fresh weight basis, respectively. Phyllodes, however, contain sufficient RuBPcase for their CERs on a leaf area basis to equal those of leaves. If CERs of leaves and phyllodes are expressed on a RuBPcase (mg dm^{-2}) basis, the rate for phyllodes is about 5 times greater than for leaves (Table 9). Data on CER (mg CO_2 $dm^{-2}h^{-1}$) RuBPcase (mg dm^{-2}) have not been found for other species. Data from

Table 9

Photosynthetic Rates of Acacia Koa Leaves and Phyllodes Expressed on the Basis of Leaf Area, Chlorophyll, and RuBPcase+

Leaf form	mg CO_2 h^{-1} dm^{-2}	mg CO_2 h^{-1} (mg Chl)$^{-1}$	mg CO_2 h^{-1} (mg RuBPcase)$^{-1}$
Leaves	24.1a++	3.26a	0.82a
Phyllodes	22.8a	5.62b	4.44b

+Ribulose-1,5-diphosphate carboxylase.

++Each value is a mean of six observations. Values in columns followed by the same letter do not differ significantly at the 0.05 level of probability.

this study indicates that some of the RuBPcase in leaves may be inactive.

Although leaves and phyllodes have similar CERs when expressed on a projected unit area basis, leaves have about 3 times the CER rate of phyllodes when expressed on a projected organ area (Table 4). Leaves have 3 times the projected area as do phyllodes. A leaf contributes at least 3 times more photosynthate for seedling growth and development as does a phyllode.

CO_2-exchange rates (CER) of both leaves and phyllodes decrease as the zenith angle of incident PPFD (θ) increases. In nature, however, the decrease in CERs is not as great as would be expected because the PPFD absorbed by leaves remains approximately constant as θ increases from 0 to 60° (Kriedeman et al. 1964). When the PPFD is in excess of or near that required to saturate photosynthesis, the small decrease in PPFD absorbed may be offset by the increase in photosynthetic efficiency at the lower PPFD levels. In addition, a reorientation of the chloroplasts with respect to the direction of incoming PPFD could result in more complete absorption of PPFD with increasing θ.

CO_2-exchange characteristics of leaves and phyllodes are affected by their morphology and anatomy. Leaves consist of many small leaflets with smooth surfaces while phyllodes have a large rough surface. The large, rough surface of phyllodes would be expected to result in lower boundary layer conductance than would be found for leaflets under the same wind conditions. Boundary layer conductance (g_a) estimated by the formula $g_a = 0.59\ L^{-0.25}\ v^{0.5}$ where L is the

leaf area (cm^2) and v the wind speed ($cm\ s^{-1}$) (Milthorpe and Moorby 1974), the boundary layer conductance was calculated for a 1 cm^2 leaflet and a 120 cm^2 phyllode at different wind speeds (Table 10).

Table 10

Calculated Boundary Layer Conductance of a Hypothetical A. Koa Leaflet and Phyllode at Different Wind Speeds

Wind speed (v)	Boundary layer conductance	
	Leaflet	Phyllodes
	$cm\ s^{-1}$	
10	1.85	0.56
40	3.70	1.12
160	7.69	2.27
640	14.29	4.55

At each wind speed, the conductance of a phyllode is only one-third that of a leaflet. The roughness of the phyllode surface and the presence of hairs initially also decrease the conductance. Sunderland (1968) found that the drag on a smooth metal replica of a wheat leaf increased when a real leaf was attached to the metal surface. The increase was about 20 percent at V = 150 $cm\ s^{-1}$, growing to 50 percent at V = 50 $cm\ s^{-1}$ because of the increasing importance of surface friction at low speeds. Phyllode conductance would be significantly less than the values shown in Table 10 because of surface roughness and area. The boundary layer conductance of a leaflet would also probably be less than the values shown in Table 10

because of the effect of adjacent leaflets on air flow. Leaflets on a pinnae may reduce air movement. Air movement across a pinnae of many leaflets may be similar to movement across an entire leaf of the same dimensions. Phyllodes have about twice the stomatal pore area as leaves and the exchange of CO_2 is controlled by the stomates. The greater pore area apparently offsets the lower conductance of phyllodes as the total leaf conductance of phyllodes is about the same as that of leaves (Table 8).

Dark Respiration Characteristics of Leaves and Phyllodes

Leaves had slightly higher dark respiration rates than phyllodes, but these differences were not statistically significant as some of the phyllodes had higher dark respiration rates than leaves. Dark respiration rates were not found for other species of Acacia. Dark respiration rates for trembling aspen and big tooth aspen leaves were 5.7 and 4.5 mg CO_2 $dm^{-2}h^{-1}$, respectively (Okafo and Hanover 1978). Although these rates were higher than those for A. koa, the rates of CO_2-uptake were also higher. The rate of dark respiration of leaves and phyllodes represented about 13 percent of the rate of CO_2-uptake. The dark respiration rates of trembling and big tooth aspen represent about 17 and 20 percent of the CO_2-uptake rates, respectively. The percentages for koa leaves and phyllodes are similar to the percentages found for leaves of many other plants (Wood and Brittain 1972).

Dark respiration can be divided into two components-maintenance (R_m) and growth (R_g) (McCree 1974). The high energy compounds derived from the maintenance component are used to sustain the plant.

The maintenance component is proportional to the dry weight of the plant (McCree 1974). Therefore, the maintenance component for phyllodes would be expected to be larger than for leaves because the specific leaf weight for phyllodes was about 1.6 times greater than for leaves. The high energy compounds and the carbon skeletons derived from the growth component are used in the synthesis of new material. The growth respiration component is proportional to the total CO_2 influx during the previous daytime period (McCree 1974). Because CER was similar for both leaves and phyllodes, R_g would also be expected to be similar for both leaf forms.

Transpiration and Conductance Characteristics of Leaves and Phyllodes

The transpiration rates of both leaves and phyllodes were determined with both leaf forms displayed perpendicular to the irradiance source. Under these conditions, the transpiration rate of phyllodes at PPFD of 1200 μmol $m^{-2}s^{-1}$ was about 90 mg $dm^{-2}h^{-1}$, almost twice the rate for leaves (Table 7). Transpiration from a leaf is a function of the absorbed irradiance. Because the total incident radiation on a vertically-displayed phyllode is about 52 percent of the incident radiation on a horizontal leaf, the radiation absorbed by a phyllode would be about one-half of that absorbed by a leaf. Therefore, the transpiration rate on a projected unit area basis for phyllodes displayed vertically would be expected to be about the same as for leaves displayed horizontally.

The transpiration rates (projected unit area) obtained for koa leaves were similar to rates reported for apple (Pyrus malus L.), pear (Pyrus communis L.), and Hazel nut (Corylus maxima L.) tree species,

which also have photosynthetic rates similar to those of koa (Hill et al. 1960). No transpiration rates were found for either leaves or phyllodes of any Acacia species.

Leaves, as a whole, transpire about 57 percent more water than do phyllodes even when phyllodes are displayed horizontally. The change from leaves to phyllodes is an apparent adaptation to drier conditions as would occur as the plant gets larger and competition occurs within and between plants.

Total leaf conductance was similar for both leaves and phyllodes (Table 8). This was unexpected because of the differences in the transpiration rate and in the morphological and anatomical characteristics between leaves and phyllodes. The boundary layer conductance for leaves would be much greater than for phyllodes because each leaflet is small, thin, and smooth, in comparison to each phyllode. The greater boundary layer conductance for leaves is apparently offset by greater stomatal conductance of phyllodes. Phyllodes have about twice the stomatal pore area per unit leaf area as leaves have. The boundary layer and stomatal conductances apparently have about equal effect as the total leaf conductance of leaves is similar to that of phyllodes.

The total leaf conductances determined for A. koa phyllodes was similar to the value of 0.5 cm s^{-1} determined for A. harpophylla phyllodes under high PPFD and adequate leaf moisture (Tunstall and Connor 1975). At low PPFD levels and adequate moisture, total diffusive conductance for phyllodes of both species was about 0.25 cm s^{-1}. In the dark, total leaf conductance of A. harpophylla

phyllodes was about 0.02 cm s^{-1}, much less than the 0.07 cm s^{-1} obtained for A. koa phyllodes. The discrepancy could be due to a higher true conductance of A. koa phyllodes than those of A. harpophylla or to incomplete stomatal closure of the A. koa phyllodes.

Ecological Significance of Leaves and Phyllodes

Continuous rapid plant growth is dependent upon continuous efficient absorption of PPFD. Plants which have horizontal leaves that are replaced by steeply-inclined leaves have an "ideal" foliage configuration for PPFD absorption (Trenbath and Angus 1975). The horizontal leaves of plants exposed to full sunlight intercept maximum PPFD. The larger leaves produce about 3 times more photosynthate than phyllodes. However, as the LAI increases and therefore mutual shading increases, PPFD penetration of the canopy decreases. A canopy of steeply-inclined leaves is able to intercept more PPFD under field conditions than can an equivalent canopy of horizontal leaves and, therefore, CERs are higher (Trenbath and Angus 1975). Heterophyllous plants like A. koa have this ideal foliage configuration. Horizontal leaves are replaced by steeply-inclined phyllodes. The leaves and phyllodes together allow koa and other heterophyllous species to be pioneering species. Koa makes rapid growth and therefore, is able to compete with other species that also become established after removal of the forest canopy.

The change from leaves to phyllodes is also an apparent adaptation to reduced moisture availability. Transpiration rates of phyllodes are less than leaves even when phyllodes are exposed to

higher than normal light levels. Organ orientation, surface, and anatomical characteristics, as previously discussed, all indicate that phyllodes are more drought resistant than leaves. Moisture loss after dark is less from phyllodes than from leaves because their stomates close after about 30 minutes in the dark, while stomates of leaves do not close until after 120 or more minutes in the dark. Tunstall and Connor (1975) found that phyllodes of A. harpophylla can carry on photosynthesis over a wider range of environmental conditions than can leaves; i.e., ambient temperatures 0 to 50^{o} C, relative humidity 20 to 100 percent, and daily radiation from 5 to 20 MJm^{-2}. Phyllodes are able to maintain a favorable internal moisture state even under adverse conditions. Therefore, phyllodes tend to persist even under very adverse conditions (Tunstall and Connor 1975). This persistence makes it possible for A. koa to exploit the environment when conditions again become favorable. Although no data are available for leaves of any Acacia species, it has been observed in the nursery that A. koa plants shed their leaves when the seedlings are stressed for moisture. If leaves are lost because of moisture stress, plant recovery, even under favorable moisture conditions, is doubtful.

CHAPTER IV

PHOTOSYNTHESIS, RESPIRATION, AND GROWTH OF *ACACIA KOA* SEEDLINGS EXPOSED TO DIFFERENT LIGHT LEVELS

Introduction

Plants are generally classified as sun or shade plants, depending on the PPFD under which they normally grow. Even where plants develop in full sun, large differences in leaf morphology and anatomy are found between leaves outside and within the interior of the canopy. Photosynthetic photon flux density also greatly affects photosynthetic and respiration rates and dry matter production. Leaf pigment content, enzyme development, and function, are highly correlated with PPFD.

Based on observations in the forest, *Acacia koa* would be classified as a sun plant because young trees are generally most abundant and vigorous in openings in the forest. However, no data are available as to the effect of PPFD on photosynthesis, respiration, and growth of koa seedlings. This study was conducted to determine the optimum irradiance for the culture of koa seedlings. The information should allow the nurseryman and forester to manipulate the light environment to enhance koa growth and development.

Literature Review

Photosynthetic photon flux density affects morphological development and dry matter production of plants (Bjorkman and Holmgren 1963, Blackman and Black 1959, Boardman 1977, Bourdeau and Laverick 1958, Friend 1980, Gordon 1969, Loach 1967). Plants growing under low PPFD have elongated internodes and spindly stems. Shade plants have

fewer but larger leaves than sun plants. Shade leaves of sun plants are larger in area, but thinner in cross section than sun leaves (Bjorkman and Holmgren 1963, Boardman 1977, Logan and Krotkov 1969, Nobel, et al. 1975). As PPFD is increased, leaves become thicker in cross section and smaller in area, stem internodes become shorter and stem diameter increases. Dry matter production rates and content increase as PPFD is increased. As a consequence of the effects of PPFD on individual plants, plant dry weight per unit of land area increases linearly with increasing PPFD. However, an increase in PPFD results in a decrease in leaf area added per unit of dry matter produced (Brix 1967). This is because leaf production and expansion rates decrease with increasing PPFD (Sajise and Lales 1976).

Photosynthetic photon flux density also affects root development because it affects the supply of photosynthate translocated to the roots (Webb 1976). Under a high PPFD, a greater proportion of the total photosynthate is translocated to the roots than under a low PPFD (Hart and Kortschak 1967, Hodgkinson and Veale 1966). Therefore, the competition for respiratory substrates between shoot and roots is less (Lister et al. 1967, McCree 1974). During periods of high photosynthesis, rates of root respiration may be 34 percent higher than rates when shoots are darkened (Szaniawski and Adams 1974).

The chlorophyll content and ultra structure of leaves varies with PPFD. Shade leaves generally have fewer chloroplasts across a leaf section, but the chloroplasts are usually larger and contain more chlorophyll (Anderson et al. 1973, Boardman et al. 1974, Goodchild et al. 1972, Holmgren et al. 1965). Leaves grown at low PPFD have

more chlorophyll per unit weight or per unit volume of leaf (Bjorkman 1975, Hoober and Stegeman 1976, Louwerse and Zweerde 1977), but the chlorophyll content per unit area of leaf surface is often lower than that of leaves grown at high PPFD (Bjorkman and Holmgren 1963, Hesketh 1968, Wild et al. 1975). The increase in size of the chloroplasts and the amount of chlorophyll per chloroplast in shade leaves is more than offset by the decrease in the number of chloroplasts per unit area of leaf surface. A change in PPFD results in changes in chloroplast ultra-structure. Grana thickness increases as PPFD decreases, but above a given PPFD no additional changes were observed (Skene 1974). The proportion of chl b relative to chl a increases as PPFD is lowered below a threshold value which is usually about the PPFD where morphological changes also occur (Bjorkman and Holmgren 1963, Boardman et al. 1972, Lewandowska et al. 1976). The higher proportion of chl b in understory species enhances their light-absorbing capacity in the wavelength region between the main blue and red bands of chl a (Boardman 1977). Leaves in the higher, more exposed part of the upperstory species have a higher proportion of chl a which allows them to utilize the blue and red wavelengths.

Shade species have lower soluble leaf protein/chl ratios than sun plants. They contain smaller amounts of RuBPcase which correlate with their low levels of soluble protein (Bjorkman 1975, Boardman et al. 1972). The rate of synthesis of RuBPcase and other enzymes involved with photosynthesis is controlled by PPFD (Salisbury and Ross 1978, Tobin and Suttie 1980). Under low PPFD, the rate of synthesis is slow. As PPFD increases to the saturation level the rate of enzyme

synthesis also increases. Photosynthetic photon flux density levels beyond the light-saturation point may be injurious.

The CO_2-exchange characteristics of individual leaves vary, depending on the PPFD under which they developed. Sun leaves of trees are light-saturated at PPFD of 600 to 900 μmol $m^{-2}s^{-1}$. Shade leaves, however, are accustomed to low PPFD and become light-saturated at PPFD only one-fourth to one-third of those required to light-saturate sun leaves. Generally, light-saturated CERs of most plants are considerably higher for sun leaves (16 to 20 mg CO_2 $dm^{-2}h^{-1}$) than for shade leaves (2 to 5 mg CO_2 $dm^{-2}h^{-1}$). The light compensation points of sun leaves are also higher than for shade leaves being 20 to 30 μmol $m^{-2}s^{-1}$ and 2 to 10 μmol $m^{-2}s^{-1}$, respectively (Berry 1975, Boardman 1977, Boehning and Burnside 1956). Shade leaves can usually photosynthesize at higher rates under low PPFD than can sun leaves (Salisbury and Ross 1978).

Leaves on the same plant may have CO_2-exchange characteristics of sun leaves, shade leaves, or both, depending on their exposure. Leaves on the shaded side of plants growing under a high PPFD (shade leaves) have characteristics more like those of leaves on true shade plants than do the sun leaves on the sunny side. These differences result from anatomical and biochemical adaptations during leaf development as previously noted.

Sun plants generally are incapable of growth or only grow slowly at PPFD as low as those tolerated by extreme shade plants. Conversely, species or ecotypes limited in nature to densely-shaded habitats lack the genetic ability to produce photosynthetic machinery

as efficient at high PPFD as that of sun plants and their leaves may even be damaged at high PPFD levels (Bjorkman 1975, Boehning 1949, Bormann 1953, Kozlowski 1949). Kozlowski (1957) found much greater inhibition of photosynthesis by PPFD over time in hardwood seedlings than in pine seedlings. He suggested that in well-exposed trees, inhibitory solarization may cause the outer leaves of tree crowns to photosynthesize less efficiently than do partially-shaded leaves. The decrease in photosynthetic efficiency was caused by photo-oxidative deactivation of some enzymes. A further decline in photosynthetic efficiency with time was caused by photo-bleaching of the chlorophyll or a combination of the two factors. Continuous exposure of plants to high PPFD can reduce their growth (Krueger and Ferrell 1965), or kill them (Ronco 1970, Ronco 1972).

Forest trees are generally classified as shade-tolerant or intolerant, depending on the PPFD under which they grow. Shade-tolerant species generally photosynthesize more efficiently at lower PPFD than intolerant species, and therefore, they are generally found as understory species or as climax types. Shade-intolerant species are commonly found in open areas such as would occur after some disturbance; i.e., fire or logging. The different photosynthetic rates of various species at different PPFD affect their ability to compete. Species composition of a forest is ultimately determined by adaptation of the different species to PPFD. Kramer and Decker (1944) found that the photosynthetic rate of shade-intolerant loblolly pine seedlings increased with PPFD up to almost full sunlight whereas the photosynthetic rate of three shade-tolerant hardwood species saturated

at less than one-third of full sunlight. Their results indicated that the lack of sufficient light for maximum photosynthesis may be a factor in the failure of pine seedlings to become established under forest stands. They speculated that pine seedlings grown in shade were unable to manufacture enough food to develop a root system large enough to absorb adequate water during periods of drought. Certain hardwood species, on the other hand, carry on relatively higher rates of photosynthesis in shade and therefore can develop more extensive root systems, probably thus enabling them to survive droughts which are fatal to pine seedlings.

Logan (1973) concluded from a study of the height and dry weight increase of 22 tree species grown under four different PPFDs, that shade-tolerant species have inherently slower growth rates than intolerant species. He also concluded that shade-tolerant species maintain relatively better root growth than intolerant species.

Wilson and Fischer (1977) found that growth of striped maple (Acer pennsylvanicum) was directly related to PPFD. Striped maple may persist in the understory for 20 or more years and when PPFD becomes sufficient, it begins to grow rapidly. At PPFD of less than 10 percent of full sunlight, bud scales were formed; at 18 percent, leaves were formed. Maximum growth in height and the formation of paired leaves occurred at 30 to 40 percent of full sunlight.

Materials and Methods

Establishment and Growth of Seedlings

Seed was collected from several mature trees growing at 1600-m elevation on Mount Hualalai on the island of Hawaii. Seedlings for

this study were grown in the greenhouse at the University of Hawaii Experiment Farm in Waimanalo, island of Oahu. The study began November 7, 1980 and was completed April 17, 1981. The sunlight levels (outside) and the temperature and relative humidity inside the greenhouse during the study period are given in Appendix A. The sunlight level inside the greenhouse was about 70 percent of that outside as determined with a Lambda Instruments Inc. LI-190 quantum sensor. The seed was sized and scarified by the hot water treatment as specified in Chapter 1. One imbibed seed was sown into a plastic tube[1] 2 cm wide by 12.5 cm deep. The rooting medium was peat moss and vermiculite, 1 to 1 by volume. The seeds were covered with crushed basalt rock about 4 mm in size. The tubes were placed in the greenhouse and the seeds germinated in 100, 77, 45, and 27 percent of the maximum light level inside the greenhouse. The 100 percent light level is considered adequate for most plants where little mutual shading within or between plants occurs (Warrington et al. 1978). The reduced light levels were established using neutral density saran screen.

About 3 weeks after germination, 90 uniform seedlings from each light level were transplanted into 15 cm wide by 18 cm deep plastic pots. The rooting medium was peat moss and vermiculite, 1 to 1 by volume. The seedlings were replaced under the light level at which they were germinated. About 6 g of Osmocote fertilizer (14-14-14)

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[1]Hawaii dibbling tubes are used for the production of forestation stock in Hawaii (Walters and Horiuchi 1979).

were placed on the surface of the growing media in each pot. The 90 seedlings at each light level provided a pool from which seedlings were selected for gas exchange determinations and growth analyses. The bases for seedling selection were average-sized healthy plants.

Gas Exchange Determinations

CO_2-uptake and CO_2-efflux (dark) determinations were made every 3 weeks on six seedlings from each treatment. The first determinations were made at the time the seedlings were potted; the last were made when the seedlings were 18 weeks old. The materials and methods for determining CERs were the same as described in Chapter III, except determinations were made only at PPFDs of 1250 and 165 $\mu mol\ m^{-2}s^{-1}$ and in darkness.

Chlorophyll, Total Soluble Protein, and Ribulose-1,5-diphosphate Carboxylase Determinations

When the seedlings were 18 weeks old, the levels of chlorophyll, TSP, and RuBPcase in the fourth or fifth leaf (LPI-4 or 5) of six seedlings from each PPFD treatment were determined. The materials and methods were as described in Chapter III.

Seedling Growth Determination

Every 3 weeks, after CO_2 exchange determinations were made, the potting media was washed from the roots of nine seedlings from each treatment. Measurements were made of stem height and diameter, leaf area and number, and dry weight of the stem, leaves, and roots. Dry weights were determined after several days of drying at 70° C. Total biomass was determined by adding the dry weights of roots, shoot, and leaves.

Relative growth rate (RGR), NAR, and LAR were calculated from these data.

Data Analyses

The means and standard deviations for the CER, chlorophyll, TSP, and RuBPcase, were determined from the six seedlings in each treatment. Treatment means were compared using Tukey's LSD (0.05 level) value. The means and standard deviations for stem height and diameter, leaf number and area, and dry weights, and for RGR, NAR, and LAR, were determined from nine seedlings in each light level. These treatment means were also compared using Tukey's LSD (0.05 level) value. All differences reported as significant are significant at least at the 0.05 level.

Results

Seedling Growth and Development

Stem height and diameter growth were significantly affected by light level. After 42 days, differences in stem height and diameter between the treatments were already evident (Table 11). Seedlings in 45 percent light were significantly taller than those grown in 100 percent light. Seedlings in the 77 and 27 percent treatments were also taller than those grown in the 100 percent treatment, but the differences were not significant. Stem diameter decreased as the light level was decreased, but the differences at 42 days were not significant. With each succeeding measurement, there was greater separation in stem height and diameter between the treatments. Seedlings grown in the 100 percent treatment always had significantly greater stem height and diameter than seedlings grown in the 27

Table 11

Stem, Leaf, and Root Development of Acacia Koa Seedlings Grown Under Different Light Levels

Days since emergence	Light level	Stem		Leaves		Area leaf	Dry weight				Shoot- root ratio
		Height	Diameter	Number	Area		Stem	Leaves	Roots	Total	
	Percent	- - - cm - - -			- - cm^2 - -		- - - - - - - gram - - - - - - -				
42	100[+]	21.4a[++]	0.29a	8.3ab	100.5a	12.1	0.16a	0.36a	0.13a	0.66a	4.1a
	77	22.4ab	0.28a	8.2a	104.1a	12.7	0.21a	0.45a	0.15a	0.81a	4.5a
	45	25.4b	0.27a	9.5b	113.5a	12.0	0.23a	0.47a	0.14a	0.84a	5.4a
	27	23.3ab	0.23a	7.3a	94.2a	12.0	0.20a	0.38a	0.14a	0.73a	4.5a
68	100	35.4a	0.40a	11.3a	234.7a	20.8	0.54a	0.88a	0.31ab	1.72a	4.7a
	77	33.9ab	0.38a	10.1ab	241.8a	23.9	0.50a	0.87a	0.34a	1.70a	4.1a
	45	35.0ab	0.37a	11.3a	246.0a	21.8	0.42a	0.75a	0.21b	1.38a	6.0a
	27	28.5b	0.29b	8.9b	140.8b	15.8	0.20b	0.39b	0.10	0.70b	5.9a
93	100	60.7a	0.59a	15.4a	335.0a	21.8	1.69a	2.24a	0.89a	4.82a	4.7a
	77	54.3a	0.56ab	13.3ab	374.4a	28.2	1.30ab	1.81ab	0.64ab	3.75ab	4.9a
	45	54.3a	0.48b	13.0b	344.3a	26.5	1.06bc	1.36bc	0.45bc	2.87b	5.8a
	27	39.8b	0.34c	12.1b	234.3a	19.4	0.61c	0.70c	0.22c	1.54c	6.1a
107	100	77.0a	0.74a	18.4a	624.6a	34.0	3.14a	4.07a	1.50a	8.70a	5.4a
	77	71.4a	0.65b	17.7a	544.2a	30.8	2.52a	2.58b	1.03a	6.14b	5.2a
	45	70.0a	0.61ab	17.0a	636.7a	37.4	2.36a	2.69b	0.97a	6.02b	5.3a
	27	46.0b	0.41c	13.4b	224.1b	16.7	0.72b	1.01c	0.32b	2.06c	5.6a
131	100	89.7a	0.80a	18.3a	793.7a	43.4	5.54a	4.25a	2.00a	11.79a	5.0a
	77	91.2a	0.81ab	16.1ab	815.5a	50.6	5.66a	4.36a	1.92ab	11.94a	5.6a
	45	77.5b	0.65c	17.4a	714.7a	41.0	3.24b	3.48a	1.10b	7.81b	6.8a
	27	38.7c	0.69bc	12.3b	310.4b	25.2	1.22c	1.28b	0.41c	2.92c	6.1a
161	100	111.3a	0.91a	17.7ab	728.4a	41.1	7.94a	4.41a	2.68a	15.02a	4.8a
	77	102.2a	0.77b	17.8ab	641.2ab	36.0	5.40b	3.32b	1.62b	10.33b	5.6ab
	45	86.1b	0.62c	19.6a	503.0b	25.6	3.12c	2.55b	0.87c	6.55c	6.8b
	27	55.3c	0.49d	14.2b	217.4c	15.3	1.18d	1.12c	0.46d	2.76d	5.2ab

[+]The light level in the fiberglass-covered greenhouse at midday is about 70 percent of that outside.

[++]Each value is a mean of nine observations. Values in columns for a time period followed by the same letter are not significantly different at the 0.05 level of probability.

percent light treatment. The stem height and diameter of seedlings grown in the 77 and 45 percent treatments were generally intermediate between seedlings in the other two treatments. After 161 days, both stem height and diameter were greatest for seedlings grown in the 100 percent treatment. Both stem height and diameter decreased as light level decreased. Seedlings grown in the 100 percent treatment were more than twice as tall and had stem diameters about 86 percent larger than seedlings grown in the 27 percent light treatment (Table 11).

The number of leaves on a seedling in each treatment increased until about the 107th day after germination (Table 11). Thereafter, the number remained static indicating some leaves were lost as others were gained or growth was slowed. Seedlings in the 27 percent treatment consistently had fewer leaves than seedlings in the other treatments. However, in many cases, leaf number was not significantly affected by light treatment, primarily because of the large amount of variability within treatments.

Differences in leaf area due to light treatment generally were small and only a few of the differences between the 27 percent treatment and all others were significant (Table 11). Leaf area of seedlings in each treatment increased with time up to the 131st day after which average leaf area declined. The decrease in leaf area was due to the fact that there was less area per leaf rather than because of fewer leaves per stem, except for the 100 percent light treatment.

Phyllodes began to develop on seedlings in the full sunlight treatment during the growth period between days 131 to 161. Phyllodes did not develop on seedlings in the other treatments.

The dry weight increase of seedlings varied with time and light treatment. After 42 days, there were no significant differences in stem, leaf, or root dry weights due to treatment (Table 11). By 68 days after emergence, the stem, leaf, and root dry weight of seedlings in the 27 percent light treatment were all significantly less than those in the other treatments. At each succeeding measurement time, differences in dry weights of stem, leaves, and roots of seedlings due to treatment increased (Fig. 8 and Table 11). The data of Figure 8 show the increase in stem, leaf, and root dry weight in the different treatments. The decrease in the dry weight of stem, leaves, and roots of seedlings in the 77 percent treatment after 131 days may be due to sampling error or to inter- and intra-plant competition. The decreases in dry weights of seedlings in the 45 and 27 percent light treatments are thought to reflect actual decreases due to a general loss of vigor. Some of the larger leaves were lost and replaced by ones that were smaller and more succulent.

The following is an average number of times (1X) that seedlings in the 100 percent light treatment were larger than those in the other treatments in terms of stem, leaf, root, and total dry weight:

Percent light	Stem	Leaves	Roots	Total
100	1.0	1.0	1.0	1.0
77	1.5	1.3	1.6	1.4
45	2.5	1.7	3.1	2.3
27	6.7	3.9	5.8	5.4

Although there were significant differences in stem, leaf, and

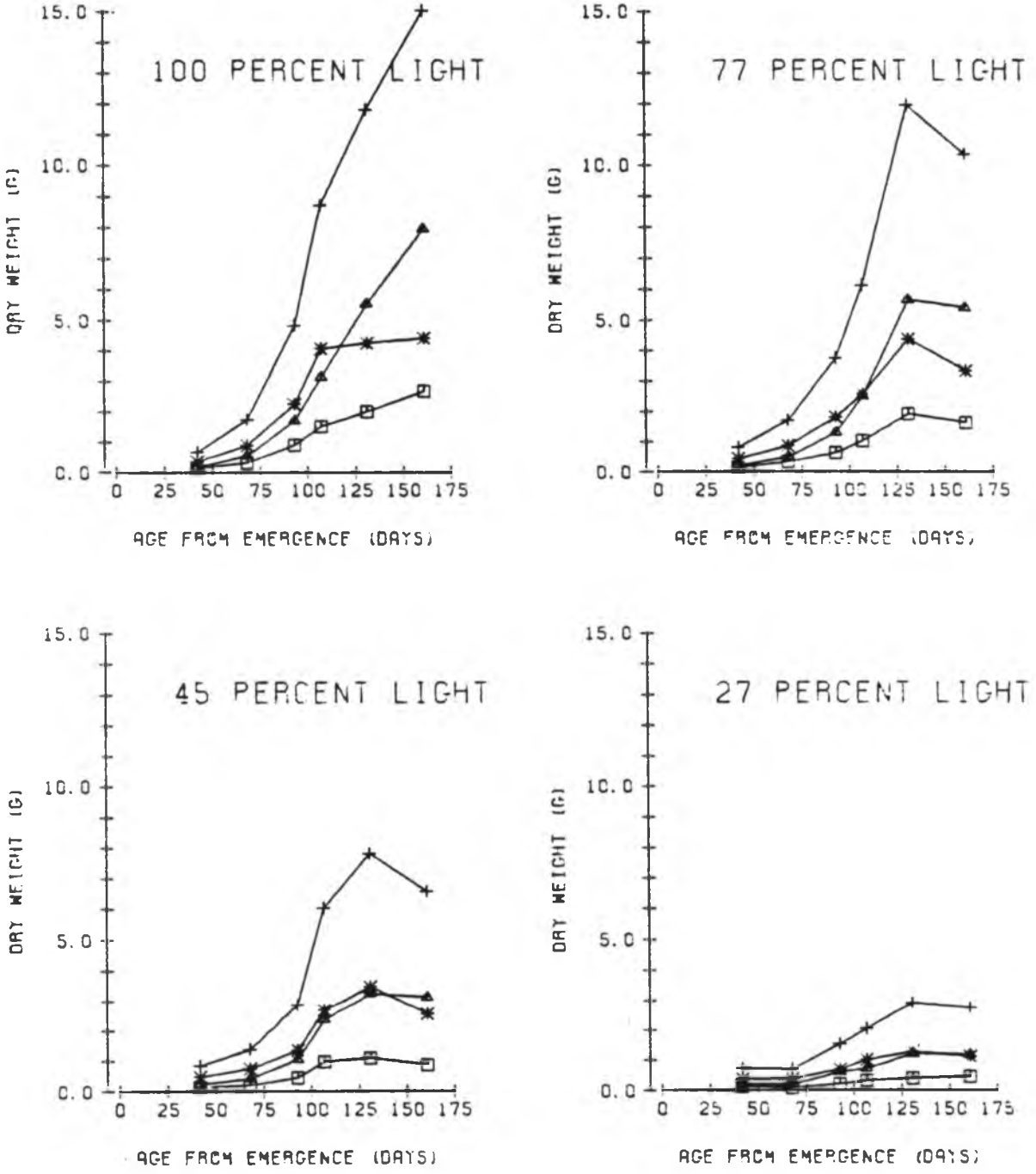

Figure 8. Dry weight increments of stem (Δ), leaves (*), roots (□), and total (+) of Acacia koa seedlings grown under different light treatments.

root dry weight due to treatment, differences in dry weight of stems, leaves, and roots, as a percent of total dry weight, were not significantly affected by treatment (Table 12). After 42 days, leaves, stems, and roots made up about 55, 26, and 19 percent, respectively, of the total dry weight of seedlings in each treatment. At each measurement time, the percent in stems increased. The percent of total dry weight in roots remained almost constant over time. After 161 days, stems made up about 49 percent of the total dry weight, leaves 35 percent, and roots 16 percent.

Growth Analysis Components

Koa relative growth rates (RGR) (or the biomass increment per unit of existing biomass) were generally similar for seedlings in each light treatment (Table 13). Relative growth rates decreased significantly with decreasing light level only during the growth period between days 42 and 68. The negative RGR for seedlings in the 27 percent light treatment during that growth period, and for seedlings in the 77, 45, and 27 percent light treatments in the growth period between days 131 and 161, was due to a decrease in mean total dry weights of the seedlings at the end of the respective growth periods (Fig. 8 and Table 11). The RGR of seedlings in the 100, 77, and 45 percent light treatments peaked during the 93- to 107-day growth period, whereas the RGR of seedlings in 27 percent light treatment peaked during the 68- to 93-day growth period.

The NAR (the biomass increment per day per unit leaf area) of the seedlings in the 100 percent light treatment in each growth period, except for the period from day 107 to 131, was significantly greater

Table 12

Dry Weight Distribution in Stems, Leaves, and Roots of *Acacia Koa* Seedlings Grown Under Different Light Levels

Days since emergence	Light level	Percent of total dry weight		
		Stem	Leaves	Roots
		- - - - - - - - - Percent - - - - - - - - -		
42	100	26	55	20
	77	26	55	19
	45	27	56	17
	27	27	54	19
68	100	31	51	18
	77	29	51	20
	45	30	54	16
	27	29	56	15
93	100	35	46	19
	77	35	48	17
	45	37	47	16
	27	40	45	15
107	100	36	47	17
	77	41	42	17
	45	39	45	16
	27	35	49	16
131	100	47	36	17
	77	47	37	16
	45	41	45	14
	27	42	44	14
161	100	53	29	18
	77	52	32	16
	45	48	39	13
	27	43	40	17

Table 13

Growth Analysis Components for *Acacia Koa* Seedlings Grown Under Different Light Levels

Component	Light level	Growth period (days) 42-68	68-93	93-107	107-131	131-161
	Percent					
Relative growth rate ($g\ g^{-1}d^{-1}$)	100	0.036a[+]	0.045a	0.046a	0.013a	0.008a
	77	0.028a	0.033a	0.35a	0.028a	-0.005a
	45	0.019ab	0.030a	0.044a	0.010a	-0.006a
	27	-0.002b	0.032a	0.021a	0.014a	-0.002a
Net assimilation rate ($mg\ cm^{-2}d^{-1}$)	100	0.248a	0.440a	0.596a	0.182ab	0.141a
	77	0.210ab	0.270b	0.376b	0.360a	-0.074b
	45	0.121bc	0.204b	0.415b	0.111b	-0.070b
	27	-0.010c	0.183b	0.162c	0.135b	-0.020b
Leaf area ratio ($cm^{-2}g^{-1}$)	100	144.4a	103.0a	70.6a	69.6a	57.9a
	77	135.4a	121.0b	94.2b	78.4a	65.2a
	45	156.7a	149.2b	105.8b	91.5b	84.2b
	27	165.0a	176.6c	130.4c	107.4b	92.6b

[+]Each value is a mean of nine observations. Values in columns for a growth analysis component followed by the same letter are not significantly different at the 0.05 level of probability.

than for seedlings in 27 percent light treatment. The NAR of seedlings in 77 and 45 percent light treatments generally fell between the other two treatments. The NAR of seedlings peaked at the same growth periods as did RGR.

The LAR (the ratio between leaf area and total dry weight) increased significantly with decreasing light for each growth period, except the first (Table 13). The largest LAR values in 100, 77, and 45 percent light were found for growth period from day 42 to 68. The LAR of seedlings in the 27 percent light treatment was largest during the 68- to 93-day growth period. As the seedlings grew, a higher percentage of dry matter accumulated in the stem than in the leaves (Table 12). This is reflected in the decreasing LAR values with time for seedlings in each treatment.

CO_2-Exchange Rates

The CER, when determined at 1250 μmol $m^{-2}s^{-1}$, was always greatest for seedlings grown in the 100 percent light treatment and least for those grown in the 27 percent light treatment. These differences were generally significant (Table 14). The CER of seedlings in the 77 and 45 percent light treatments were generally intermediate to those for the 100 and 27 percent light treatments. The significantly lower CER values for seedlings in the 77, 45, and 27 percent light treatments at 42 days and the 77 percent light treatment at 68 days probably resulted from making CER determinations on immature leaves. At this stage the oldest, apparently fully expanded leaves were used. These were generally LPI 3 or 4. As the study progressed, LPI 4 or 5 was used to ensure that only fully-expanded

Table 14

CO_2-exchange Rate by a Single Fully-expanded *Acacia Koa* Leaf Grown Under Different Light Levels

Days since emergence	Light level	CER at measurement PPFD		
		1250	165	Dark
	Percent	- - - mg CO_2 $dm^{-2}h^{-1}$ - - -		
42	100	23.62a+	--	-2.51a
	77	17.41b	--	-1.49b
	45	15.54bc	--	-1.32b
	27	12.90c	--	-1.39b
68	100	27.47a	9.33a	-2.97a
	77	20.52b	8.77a	-2.18b
	45	21.77b	10.22a	-2.13b
	27	20.48b	9.30a	-1.87b
93	100	27.02ab	9.22a	-2.73a
	77	28.34a	10.58a	-2.34ab
	45	26.92ab	11.14a	-1.92b
	27	22.96b	10.62a	-1.75b
107	100	26.88a	9.41ab	-2.13a
	77	25.12ab	11.73a	-1.91a
	45	22.14bc	11.69a	-1.65b
	27	17.70c	8.71b	-1.48b
131	100	30.10a	10.44a	-2.43a
	77	29.88a	11.66a	-1.99b
	45	24.39ab	10.03a	-1.52b
	27	18.57b	10.34a	-1.68b
161	100	22.66ab	5.00a	-2.89a
	77	23.96ab	5.82a	-2.25b
	45	24.56a	5.96a	-2.13b
	27	19.81b	5.79a	-2.04b

+Each value is a mean of six observations. Values in columns for a time period followed by the same letter are not significantly different at the 0.05 level of probability.

leaves were used.

The CER of seedling leaves determined at 165 μmol $m^{-2}s^{-1}$ was similar for each treatment. Koa seedlings grown at low light were not significantly more efficient in fixing CO_2 at low PPFD than those grown at high light although the CER of seedlings grown in the 45 percent treatment had higher CERs than those grown in the 100 percent light treatment. The CER measured at 161 days in a PPFD of 165 was only about one-half the rate obtained at all other measurement times (Table 14). There is no explanation for this decrease but it was consistent for seedlings in all light treatments.

The CERs determined in the dark (respiration) were consistently highest for seedlings grown in the 100 percent light treatment and decreased as the light level decreased (Table 14). The differences in dark respiration rate between seedlings in the 100 and 77 percent light were generally significant. However, dark respiration rate differences between the 77, 45, and 27 percent light treatments were not significant. There were no correlations between the dark respiration rate and CER at light-saturation for seedlings grown at any light level.

Leaf contents of chl a, b, and total varied with treatment (Table 15). Leaves from plants grown in the 45 percent light treatment had significantly more chl a, b, and total than leaves from the 77 percent light treatment, which in turn had significantly more chlorophyll (a, b, total) than leaves from plants grown in the 100 percent treatment. Leaves in the 27 percent light treatment were the exception as they had chl b levels similar to those leaves from the 77 percent light

Table 15

Chlorophyll Content of Acacia Koa Leaves
Grown Under Different Light Levels

Light level	Chlorophyll a		Chlorophyll b		Chlorophyll Total		a/b
	mg g^{-1}	mg dm^{-2}	mg g^{-1}	mg dm^{-2}	mg g^{-1}	mg dm^{-2}	
100	1.25a+	2.15a	0.55a	0.94a	1.80a	3.09a	2.30a
77	1.61b	2.37a	0.72ab	1.05ab	2.34b	3.42a	2.24ab
45	1.87c	2.32a	1.00c	1.24b	2.87c	3.55a	1.87b
27	1.64b	2.22a	0.81bc	1.09ab	2.45b	3.32a	2.02ab

+Each value is a mean of six observations. Values in columns followed by the same letter are not significantly different at the 0.05 level of probability.

treatment. The ratio of chl a to b decreased as the light level decreased.

The TSP and RuBPcase levels of leaves were not significantly correlated with treatment. Leaves grown in the 100 percent light treatment had significantly more TSP and RuBPcase than leaves grown at the other light treatments, but there were no significant differences between TSP and RuBPcase levels and among the other treatments (Table 16). The RuBPcase comprised about 42 percent of the TSP regardless of the light regime of the plants.

Discussion

Seedling Growth and Development

The quantity of available light afforded by the four treatments affected the length of the establishment period and the subsequent

Table 16

Total Soluble Protein and RuBPcase[+] Content of *Acacia Koa* Leaves Grown Under Different Light Levels 161 Days After Emergence

Light level	Total soluble protein		RuBPcase[+]	
Percent	mg g^{-1}	mg dm^{-2}	mg g^{-1}	mg dm^{-2}
100	44.87a[++]	79.37a	18.33a	32.32a
77	37.33b	52.57b	16.45ab	23.17b
45	35.00b	42.75b	14.63b	18.02b
27	36.80b	50.88b	16.07ab	22.33b

[+]Ribulose-1,5-diphosphate carboxylase.

[++]Each value is a mean of six observations. Values in columns followed by the same letter are not significantly different at the 0.05 level of probability.

rate of growth as shown by increased stem height and diameter, and component and total dry weights. The highest light level in the greenhouse was only 70 percent of full sunlight. Perhaps the length of the establishment period could have been shortened and subsequent growth rates increased by growing seedlings outside the greenhouse. Koa grows naturally under full sunlight so no detrimental effects of high PPFD levels would be likely.

Low light levels usually stimulate height growth at the expense of diameter growth and stem strength and sturdiness (Reifsnyder and Lull 1965). However, in this study, koa seedling growth in height and stem diameter were positively correlated with the available light.

The dry weight increase of stems and roots of several temperate-zone conifers has been found to be episodic and alternating (Krueger

and Trappe 1967, Ledig et al. 1976). Therefore, root dry weight increase was rapid while stem dry weight increase was nil. After some time, stem dry weight increase became rapid and root dry weight increase became nil. Koa seedlings, however, did not exhibit either episodic or alternating stem and root growth. Stems and roots of koa seedlings grew at the same time. As koa seedlings grew, the proportion of the total dry weight in stems, including leaves, and roots remained at about 80 and 20 percent, respectively. This would explain the relatively constant shoot-root ratios shown in Table 11. As koa seedlings grew, the percentage of total dry weight made up of leaves decreased while the percentage of total dry weight made up of stem increased. These growth characteristics of koa occurred regardless of growth PPFD. Leaves were not lost from seedlings in the 27 percent light treatment as would occur if the light level was below the light compensation point. The constant percentage of roots was apparently not due to a restricted root environment or lack of water and nutrients because supplies were ample and there was still space for growth within the container at the final harvest date.

Studies with other species have shown that NAR increased and LAR decreased with increasing light (Blackman and Black 1959, Friend 1969, Warrington et al. 1978) and similar results were obtained in this study. The decrease in LAR with increasing light can be attributed to a greater proportion of dry matter being distributed to plant parts other than leaves (Table 12) and to thicker individual leaves being produced on the plant. Relative growth rate did not change greatly with increases in light level, principally because its components, NAR

and LAR, both changed with available light in a manner that maintained a near constant RGR. Similar results were obtained by Warrington et al. (1978) for both C_3 and C_4 species.

The RGR, NAR, and LAR values obtained for koa were typical of C_3 plants in general, as they were similar to values obtained for cotton (Mauney et al. 1978), walnut (Juglans nigra L.), honeylocust (Gleditsia triacanthos L.) (Carpenter and Hanover 1974), and for northern red oak (Quercus rubra L.) (Farmer 1975).

CO_2-Exchange Rate

For plants adapted to full sunlight (nonshade plants), the CER of leaves at light saturation usually is higher for leaves that developed under full sunlight than it is for leaves that developed in deep shade. Conversely, the CER of leaves in low light is higher for leaves that developed in shade than for leaves that developed in full sunlight (Berry 1975, Bjorkman et al. 1972). The former case was true for koa leaves, but koa leaves that developed at 27 percent of the full sunlight treatment did not have a higher CER at low light (165 $\mu mol\ m^{-2}s^{-1}$) than leaves that developed in full sunlight. The greater CER of koa leaves grown in the 100 percent light treatment at 1250 $\mu mol\ m^{-2}s^{-1}$ can probably be partially attributed to their higher RuBPcase levels (Table 14). Boardman (1977) reported that other factors that contributed to a higher CER at high light are higher levels of constituents of the electron transport chain and greater mesophyll and stomatal conductances. Though no measurements of these components were made on koa leaves, it seems likely that similar results to those reported by Boardman (1977) would have been

obtained. The leaf morphology of leaves grown under high light results in greater stomatal and mesophyll conductances to CO_2 than is found for leaves grown under low light. The increased stomatal conductance is correlated with a greater stomatal frequency (Bjorkman et al. 1975, Charles-Edwards and Ludwig 1975, Crookston et al. 1975) and mesophyll conductance is proportional to leaf thickness and the surface area of the mesophyll cells, both of which increase when leaves develop in a high light environment (Holmgren 1968, Nobel et al. 1975). Leaves which develop in high light also have a higher overall cell metabolism than do leaves that develop under low light (Boardman 1977) and higher dark respiration rates were measured for koa leaves grown in full sunlight than for those grown under low light (Table 14).

With koa, as with other species (Goodchild et al. 1972) the amount of chlorophyll increased as the available light decreased down to 45 percent of full sunlight. The higher chlorophyll in plant leaves grown under low light enhances energy absorption at low light, and therefore, the CER for shade leaves at low PPFD should be greater than for sun leaves. Koa leaves grown at 27 percent of full sunlight had significantly less chlorophyll than leaves grown at 45 percent of full sunlight. This is the opposite of what was expected. Although the light compensation point for individual koa leaves is about 25 $\mu mol\ m^{-2}s^{-1}$ (Chapter III), perhaps the light compensation point for the whole plant is higher. Because of mutual shading, many of the leaves may have been growing at close to the light compensation point. Under such conditions, they would not have sufficient energy

to invest in large leaves or in light-harvesting pigments. As noted earlier, the average area of a leaf in the 27 percent light treatment was about 60 percent of the area of a leaf in the 45 percent light treatment, and only about 50 percent of the area of a leaf in the full sunlight treatment.

CO_2-Exchange Rate and Seedling Growth

Plant growth is dependent on the supply of photosynthate. However, the correlation between photosynthesis per unit of leaf area and growth is often poor (Evans 1975, Helms 1976, Ledig and Perry 1967, Mauney et al. 1978). In this study, correlations between CER of single leaves and stem height and diameter, and stem, leaf, and root dry weights were also poor, with r values ranging from 0.07 to 0.18. The poor correlation was not surprising because there were few significant differences among CER values at 1250 μmol $m^{-2}s^{-1}$ for leaves grown at the different light levels.

The correlation between CER and growth probably could have been improved if the CER had been determined on whole plants instead of on single leaves. The CER varies with PPFD and PPFD varies with position in the seedling crown (Okafo and Hanover 1978). Leaves in the upper part of the crown absorb much of the incident PPFD, allowing less for the lower leaves. If the light level during growth was sufficiently great to penetrate to the lower leaves, many of these leaves would be light-saturated. However, if the growth PPFD were lower than that required for light saturation of the upper leaves, the lower leaves could be at or even below the light compensation point. The total photosynthate available for maintenance of tissue integrity and

function and for growth and development of new tissue would be greatest for seedlings that had much of their crown light-saturated.

CHAPTER V

ADAPTATION OF *ACACIA KOA* LEAVES AND PHYLLODES TO CHANGES IN AVAILABLE LIGHT

Introduction

The amount of sunlight available to a leaf often changes during plant ontogeny. Such changes are generally greatest when the plant is young because of planned or unplanned occurrences. In koa nursery culture, shade is provided during germination and early seedling development. The shade is eventually removed and the seedlings are suddenly exposed to full sunlight. Seedlings are then grown in the nursery under full sunlight until they are ready for field planting. They are sent from the nursery to the forest and planted there under full sunlight. Natural koa seedlings also develop under full sunlight. Both planted and natural seedlings often become shaded by competing vegetation. The decrease in available light resulting from competition is gradual. However, when competition is reduced, the increase in light levels is sudden. Leaves, both those partially- and fully-developed, often must adapt to changes in irradiance during ontogeny. The adaptive potential, in terms of physiology and morphology, determines whether or not a leaf is injured by a change in irradiance. Leaves with little adaptive potential may be damaged by increases or decreases in irradiance, while leaves with greater adaptive potential may not. At present, the adaptive potential of koa is not known. Therefore, the nurseryman and forester do not know how to manipulate the light environment to enhance seedling growth and development.

To investigate the adaptive potential of koa one must examine the physiological and anatomical changes that occur in both leaves and phyllodes as the amount of available light energy changes.

The objective of this study was to determine the adaptive potential of partially- and fully-developed leaves and phyllodes of koa to changes in light levels. Specifically, the changes in CER, in level of chlorophyll, TSP, RuBPcase, and specific leaf weights that resulted from changes in light levels, were determined.

Literature Review

The photosynthetic properties of a species can be modified by growing it under PPFDs different than normal; i.e., by growing a sun plant in the shade or conversely a shade plant in the sun (Bjorkman and Holmgren 1966, Bunce et al. 1977, Burnside and Boehning 1957). The extent of modification depends on the species or the variety within a species. The photosynthetic rate of some sun plants grown under shade light-saturated at a PPFD at least 20 μmol $m^{-2}s^{-1}$ lower than if they were grown under full sunlight, while rates of other species remained unchanged (Burnside and Boehning 1957). The light compensation point of sun plants grown in the shade decreased by as little as 0 and as much as 20 μmol $m^{-2}s^{-1}$. When shade plants were grown under higher than normal irradiances, the photosynthetic rate became light-saturated at higher intensities in some species, but not in others (Burnside and Boehning 1957). These modifications in photosynthetic properties resulted from physiological and anatomical changes that occurred with changes in PPFD. Leaf adaptation to a new light environment results in changes in the photosynthetic rate at a

given PPFD, stomatal conductance, leaf anatomy, leaf-water potential, photosynthetic unit size, and glycolate oxidase and RuBPcase activity. Some changes may occur within 1 day of alteration of the light environment. Changes in chlorophyll content, numbers of photosynthetic units, specific leaf weight, and malate dehydrogenase activity are slower (Alberte et al. 1976, Bowes et al. 1972, Bunce et al. 1977, Charles-Edwards and Ludwig 1975, Patterson et al. 1977). Both anatomical and physiological changes may occur even after leaf expansion is complete (Bunce et al. 1977).

Although the intrinsic photosynthetic capacity of individual leaves imposes an upper limit on a tree's potential rate of dry matter production, this potential rate is rarely approached because only part of a tree canopy is ever light-saturated. Through manipulation of canopy architecture; i.e., plant spacing, species composition, and selection for leaf orientation, the horticulturist, agronomist, or forester can increase the average PPFD on lower shaded leaves and decrease it on upper exposed leaves. The net result is a greater number of leaves assimilating CO_2 at a higher average rate and with greater photosynthetic efficiency (Boardman 1977, Bunce et al. 1977).

Many silvicultural systems were developed to meet the environmental requirements of different species (Smith 1962). Species such as red maple (Acer rubrum L.) and yellow-poplar (Liriodendron tulipifera L.) can be established and make rapid growth under relatively low PPFD (Kozlowski 1949). The shelterwood system was developed for such species (Smith 1962). Under this system, some large trees of the desired species are left during harvesting to

provide cover for the next generation. The clearcut system is used for species such as Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] which requires almost full sunlight to become established (Krueger and Ruth 1969). In the clearcut system, all stems are cut from an area.

As trees grow, competition for light and other environmental factors increases. To ensure an adequate photosynthetic rate for rapid growth of the desired tree species, stand density can be regulated by periodic thinning so that sufficient PPFD is available (Smith 1962). This regulation of stand density by periodic thinning continues up to the final harvest so that the growth curve for the crop trees is as steep and smooth as is practical for a particular management system.

Materials and Methods

Establishment and Growth of Seedlings

Seed was collected from several mature trees growing at 1600-m elevation on Mount Hualalai on the island of Hawaii. Seedlings were grown at the University of Hawaii Experiment Farm in Waimanalo, island of Oahu. The study began November 7, 1980 and was completed April 15, 1981. Seedlings were grown outside, under the solar radiation, rainfall, and temperatures shown in Appendix A. The seed was sized and scarified by the hot water treatment. One imbibed seed was sown into each plastic pot that measured 15 cm wide by 18 cm deep. The rooting medium was peat moss and vermiculite, 1 to 1 by volume. No Rhizobium bacteria was added to the media because nodules developed naturally on koa roots during earlier studies. Sixty seedlings were

placed under 100 percent of full sunlight and 60 pots were placed under 27 percent sunlight. Irrigation was sufficient to keep the rooting medium moist. About 6 g of Osmocote fertilizer (14-14-14) were placed on the surface of the growing media in each pot. Emergence began 4 days after sowing and was complete 3 days later.

Light Treatments

When the plants were 3 1/2 months old, 15 of the plants growing under 100 and 27 percent of full sunlight were placed in the opposite environment. This created four treatments containing 15 plants each. Plants grown and maintained at 100 percent light were designated HH; plants grown at 100 percent light and then moved to the 27 percent light environment were designated HL; plants grown and maintained at 27 percent light were designated LL; and those grown at 27 percent light and moved to the 100 percent light environment were designated LH.

The rates of gas exchange and levels of chlorophyll, TSP, and RuBPcase were determined 7 and 28 days after the seedlings were exposed to the different light levels. Leaves used in the 7-day determinations were fully developed while those used in the 28-day determinations were partially developed when the treatments were begun. By the time the 28-day determinations were made, those leaves were also fully developed.

After 5 months growth, phyllodes had developed on the remaining 30 plants grown in full sunlight. No phyllodes developed on plants in 27 percent of sunlight. Because no phyllodes developed on seedlings in the 27 percent light environment, the only treatments for the

phyllodes were the HH and HL treatments. The same methodology used for leaves was used for plants with phyllodes.

Gas Exchange Determinations

The rates of CO_2 uptake and dark respiration were determined for five seedlings from each of the four treatments. The fourth or fifth leaf or phyllode (LPI-4 or 5) was used for the determinations. The CO_2-uptake rate of each leaf and phyllode was determined at a PPFD of 1250, 975, 325, and 115 μmol $m^{-2}s^{-1}$. Materials and methods for determining CERs were as described in Chapter III.

Chlorophyll, Total Soluble Protein, and RuBPcase Determinations

After CERs were determined, the leaves or phyllodes were harvested and chlorophyll, TSP, and RuBPcase determinations were made. Methods for the determinations were as described in Chapter III.

Experimental Design and Data Analysis

For each measurement, five seedlings were selected from each light treatment (HH, HL, LH, LL). The means and standard deviations for the CER, chl, TSP, RuBPcase, and SLW, were determined for each treatment. Bartlett's Test for homogeneity of variance for samples with 3 degrees of freedom was used to determine if sample variances could be pooled. If the sample variances were homogeneous, they were pooled and the treatment means were compared using Tukey's LSD value (0.05 level). If sample variances could not be pooled, treatment means were compared using t-tests with significance levels adjusted for multiple comparisons using the Bonferroni inequality.

All differences reported as significant are significant at least at the 0.05 level of probability.

Results

Adaptation of Leaves

Specific Leaf Weights. Fully-developed leaves in the HH treatment had a significantly higher SLW than fully-developed leaves in the LL treatment (Table 17). The leaflets of leaves in the HH treatment were smaller in area, but thicker cross section than leaflets of leaves in the LL treatment. Changing the level of available light did not result in significant differences between the SLW of leaves in the HL and HH treatments, or between leaves in the LH and LL treatments. Leaves that were only partially developed when the change in light environment occurred had SLWs that were not significantly different from leaves in the environment to which they had been moved (Table 17). Therefore, the SLW of leaves in the HL treatment was more similar to that of leaves in the LL treatment than to that of leaves in the HH treatment. Leaves in the LH treatment developed a SLW more similar to that of leaves in the HH treatment than to that of leaves in the LL treatment.

CO_2-Exchange Rates. The CERs of fully-developed leaves in the HH treatment were not significantly different from those in the LL treatment (Table 18). Transferring fully-developed leaves to a higher or lower light did not result in significant changes in CER. Two exceptions are the significant decrease in CER at 1250 μmol $m^{-2}s^{-1}$ of leaves in the HL treatment compared to those in the HH treatment, and the significant decrease in the CER determined at 115 μmol $m^{-2}s^{-1}$ for leaves in the LH treatment compared to those in the LL treatment. There were no significant differences in dark respiration of

Table 17

Changes in Specific Leaf Weight (fresh weight) of Acacia Koa Leaves and Phyllodes Exposed to Different Light Treatments

Stage of leaf Development[+]	Specific weight					
	Leaves				Phyllodes	
	Light treatment[++]				Light treatment	
	HH	HL	LH	LL	HH	HL
	- - - - - - - - - - g dm^{-2} - - - - - - - - - -					
Fully developed	1.37a[+++]	1.30ab	1.18bc	1.09c	3.57a	3.61a
Partially developed	1.42a	1.14b	1.47a	1.18b	3.56a	3.17b

[+]Stage of development when the change in light level occurred.

[++]Light treatments: HH--plants grown and maintained in full sunlight; HL--plants grown under full sunlight, then placed under 27 percent of full sunlight; LH--plants grown under 27 percent of full sunlight, then moved to full sunlight; LL--plants grown and maintained under 27 percent of full sunlight.

[+++]Each value is a mean of five observations. Values in rows for a leaf form followed by the same letter are not significantly different at the 0.05 level of probability.

Table 18

Changes in CO_2-exchange Rates of *Acacia Koa* Leaves Exposed to Different Light Treatments

Stage of leaf development[+]	Light treatment[++]	CER determined at PPFD (µmol $m^{-2}s^{-1}$)				
		1250	975	325	115	Dark
		- - - - - mg CO_2 $dm^{-2}h^{-1}$ - - - - -				
Fully developed	HH	26.5a[+++]	25.5a	16.4a	6.4ab	-1.5a
	HL	21.4b	21.4a	14.6a	6.1ab	-1.4a
	LH	23.3ab	22.6a	14.3a	5.8a	-1.6a
	LL	23.0ab	22.5a	17.1a	8.5b	-1.2a
Partially developed	HH	20.5ab	20.4a	12.8a	4.7a	-2.4a
	HL	23.0b	22.2a	14.0a	5.2ab	-2.0a
	LH	18.7a	19.5a	14.8a	6.5b	-1.8ab
	LL	17.8a	19.5a	14.7a	6.8b	-1.3b

[+]Stage of development when the change in light level occurred.

[++]See Table 15 for an explanation of the light treatments.

[+++]Each value is a mean of five observations. Values in columns for a leaf development stage followed by the same letter are not significantly different at the 0.05 level of probability.

fully-developed leaves in any of the treatments. Transferring partially-developed leaves to higher or lower light levels did not result in any significant changes in CER (Table 18). Although partially-developed leaves in the HH treatment had significantly higher dark respiration rates than those in the LL treatment, transferring them to higher or lower light did not result in significant changes in dark respiration rates. Therefore, the dark respiration rate of partially-developed HL leaves did not become more like that of LL leaves, nor did the dark respiration rate of partially-developed LH leaves become more like that of HH leaves.

Chlorophyll. For fully- and partially-developed leaves, the chlorophyll content (chl a, b, and total) was greater for leaves in the LL treatment than for those in the HH treatment (Table 19). Transferring fully-developed leaves from the HH to the HL treatment resulted in a significant increase in chl b (mg dm^{-2}). No other differences were significant. Transferring fully-developed leaves from the LL to the LH treatment significantly decreased chl b (mg g^{-1}) and total chlorophyll (mg g^{-1}). Changing fully-developed leaves from high to low or from low to high light did not result in significant changes in the chl a/b ratio. Transferring partially-developed leaves from the HH to the HL treatment resulted in significant increases in chl a (mg g^{-1}), chl b (mg g^{-1}), and chl total (mg g^{-1}). Transferring partially-developed leaves from the LL to the LH treatment resulted in significant decreases in chl a (mg g^{-1}, mg dm^{-2}), chl b (mg g^{-1}), and chl total (mg g^{-1}, mg dm^{-2}). As with fully-developed leaves, transferring partially-developed leaves from

Table 19

Changes in Chlorophyll Content of *Acacia Koa* Leaves Exposed to Different Light Treatments

Stage of leaf development[+]	Light treatment[++]	Chlorophyll a		Chlorophyll b		Chlorophyll Total		a/b
		mg g^{-1} (fwt)	mg dm^{-2}	mg g^{-1} (fwt)	mg dm^{-2}	mg g^{-1} (fwt)	mg dm^{-2}	
Fully developed	HH	1.50a[+++]	2.20a	0.63a	0.92a	2.13a	3.12a	2.41a
	HL	1.58a	2.25a	0.69a	1.06b	2.27a	3.23ab	2.30a
	LH	1.66a	2.45ab	0.75a	1.02ab	2.38a	3.52bc	2.23a
	LL	1.79a	2.51b	0.96b	1.04b	2.55b	3.50c	2.36a
Partially developed	HH	1.49a	2.50a	0.65a	1.11a	2.13a	3.59a	2.34a
	HL	1.92b	2.37a	0.94b	1.24a	2.87b	3.83a	2.06a
	LH	1.43a	2.21a	0.64a	0.99a	2.07a	3.20a	2.23a
	LL	2.09b	2.82b	1.00b	1.34a	3.09b	4.15b	2.11a

[+]Stage of development when the change in light occurred.

[++]See Table 15 for an explanation of the light treatments.

[+++]Each value is a mean of five observations. Values in columns for a leaf development stage followed by the same letter are not significantly different at the 0.05 level of probability.

high to low or from low to high PPFD did not result in significant changes in chl a/b ratios.

Total Soluble Protein and RuBPcase. Fully-developed leaves in the HH treatment had significantly more TSP (mg dm^{-2}) and RuBPcase (mg dm^{-2}) than did those in the LL treatment (Table 20). Transferring fully-developed leaves from the HH to the HL treatment resulted in a significant decrease in RuBPcase (mg g^{-1}, mg dm^{-2}), but no significant changes in TSP. Transferring fully-developed leaves from the LL to the LH treatment resulted in a significant increase in TSP (mg g^{-1}, mg dm^{-2}), but in no significant changes in RuBPcase.

Partially-developed leaves in the HH treatment had about the same amount of TSP, but significantly more RuBPcase (mg dm^{-2}) than those in the LL treatment. There were no significant changes in TSP or RuBPcase when partially-developed leaves were transferred from the HH to the HL treatment. When partially-developed leaves were transferred from the LL to LH treatment, both TSP (mg dm^{-2}) and RuBPcase (mg dm^{-2}) increased significantly (Table 20).

Total Soluble Protein/Chl Ratio. Fully-developed leaves in the HH treatment had a significantly higher TSP/chl ratio than did those in the LL treatment (Table 21). Transferring fully-developed leaves from the HH to the HL treatment did not result in significant changes in the TSP/chl ratio. However, transferring fully-developed leaves from the LL to the LH treatment resulted in a significant increase in the TSP/chl ratio. A similar increase in TSP/chl ratio was noted when partially-developed leaves were transferred from the LL to the LH

Table 20

Changes in Total Soluble Protein and RuBPcase[+] Content of *Acacia Koa* Leaves Exposed to Different Light Treatments

Stage of leaf development[++]	Light treatment[+++]	Total soluble protein		RuBPcase[+]	
		mg g^{-1} (fwt)	mg dm^{-2}	mg g^{-1} (fwt)	mg dm^{-2}
Fully developed	HH	44.08ab[++++]	61.06a	23.54a	32.62a
	HL	46.48ac	60.15a	18.54b	24.16b
	LH	50.22c	59.08a	23.20a	26.94b
	LL	39.52b	43.76b	23.60a	26.35b
Partially developed	HH	35.06a	53.16a	20.14a	27.95a
	HL	38.24a	48.35a	19.08a	29.38ab
	LH	42.48a	62.14b	15.90a	25.96a
	LL	37.98a	49.21a	21.16a	21.46b

[+]Ribulose-1,5-bisphosphate carboxylase

[++]Stage of development when the change in light level occurred.

[+++]See Table 15 for an explanation of light treatments.

[++++]Each value is a mean of five observations. Values in columns for a leaf development stage followed by the same letter are not significantly different at the 0.05 level of probability.

Table 21

Changes in the Ratio of Total Soluble Protein to Chlorophyll of Acacia Koa Leaves and Phyllodes Exposed to Different Light Treatments

Stage of leaf development[+]	Leaves				Phyllodes	
	Light treatment[++]				Light treatment	
	HH	HL	LH	LL	HH	HL
Fully developed	19.57a[+++]	18.62a	16.78a	12.50b	3.92a	2.95a
Partially developed	14.81a	12.62a	19.42b	11.85a	4.41a	3.86a

[+]Stage of development when the change in light level occurred.

[++]See Table 15 for an explanation of light treatments.

[+++]Each value is a mean of five observations. Values in rows for a leaf form followed by the same letter are not significantly different at the 0.05 level of probability.

treatment. Differences in the TSP/chl ratio between partially-developed leaves in the LL and LH treatments and in the HH and HL treatments were not significant (Table 21).

Adaptations of Phyllodes

Specific Leaf Weight. Both fully- and partially-developed phyllodes in the HH treatment had SLWs of about 3.56 (Table 17). When fully-developed phyllodes were transferred to the HL treatment, no significant change in SLW occurred. However, when partially-developed phyllodes were transferred to the HL treatment, SLW decreased significantly. Upon maturation, phyllodes in the HL treatment were broader and thinner than those in the HH treatment.

CO_2-Exchange Rates. The CERs of fully-developed phyllodes in

the HH treatment were significantly lower than those in the HL treatment at PPFDs of 1250, 975, and 325 μmol $m^{-2}s^{-1}$ (Table 20). Differences between CER of fully-developed phyllodes in the HH and HL treatments were not significant when determined at a measurement PPFD of 115 μmol $m^{-2}s^{-1}$ or in the dark. Although the CER of partially-developed leaves in the HH treatment averaged lower for all measurement PPFD than for those in the HL treatment, the differences were not significant (Table 22).

Chlorophyll. Transferring fully-developed phyllodes from the HH to the HL treatment resulted in a significant increase in chl a (mg g^{-1}, mg dm^{-2}), chl b (mg dm^{-2}), and total chl (mg g^{-1}, mg dm^{-2}) (Table 21). The ratio of chl a/b did not change significantly. Transferring partially-developed phyllodes from the HH to the HL treatment resulted in significant increases in chl b (mg g^{-1}, mg dm^{-2}) and total chl (mg g^{-1}), but not in chl a (Table 23). The chl a/b ratio did not change significantly.

Total Soluble Protein and RuBPcase. Transferring fully-developed or partially-developed phyllodes from the HH to the HL treatment did not result in any significant changes in TSP or RuBPcase (Table 24).

Total Soluble Protein/Chl Ratio. Transferring fully-developed or partially-developed phyllodes from the HH to the HL treatment did not result in any significant changes in TSP/chl ratio (Table 21).

Discussion

In the nursery and forest, the availabile light often changes because the occurrence or removal of natural or artificial shading creates different light environments. As a result, shade leaves are

Table 22

Changes in CO_2-exchange Rates of *Acacia Koa* Phyllodes Exposed to Different Light Treatments

Stage of phyllode development[+]	Light treatment[++]	CER determined at PPFD (μmol $m^{-2}s^{-1}$)				
		1250	975	325	115	Dark
		- - - - - mg CO_2 $dm^{-2}h^{-1}$ - - - - -				
Fully developed	HH	23.7b[+++]	21.0b	11.6b	4.0a	-2.4a
	HL	27.5a	25.2a	14.0a	5.6a	-1.3a
Partially developed	HH	19.5a	18.7a	11.3a	4.2a	-2.2a
	HL	21.4a	20.7a	12.8a	5.6a	-1.4a

[+]Stage of development when the change in light level occurred.

[++]See Table 15 for an explanation of light treatments.

[+++]Each value is a mean of five observations. Values in columns for a phyllode development stage followed by the same letter are not significantly different at the 0.05 level of probability.

Table 23

Changes in Chlorophyll Content of Acacia Koa Phyllodes Exposed to Different Light Treatments

Stage of phyllode development[+]	Light treatment[++]	Chlorophyll a		Chlorophyll b		Chlorophyll Total		a/b
		mg g^{-1} (fwt)	mg dm^{-2}	mg g^{-1} (fwt)	mg dm^{-2}	mg g^{-1} (fwt)	mg dm^{-2}	
Fully developed	HH	0.78b[+++]	2.96b	0.31a	1.16b	1.09b	4.13b	2.5a
	HL	0.91a	3.73a	0.34a	1.39a	1.29a	5.20a	2.6a
Partially developed	HH	0.80a	3.18a	0.28b	1.12b	1.08b	4.32a	2.8a
	HL	0.90a	3.35a	0.39a	1.44a	1.29a	4.79a	2.4a

[+]Stage of development when the change in light level occurred.

[++]See Table 15 for an explanation of light treatments.

[+++]Each value is a mean of five observations. Values in columns for a phyllode development stage followed by the same letter are not significantly different at the 0.05 level of probability.

Table 24

Changes in Total Soluble Protein and RuBPcase[+] Content of *Acacia Koa* Phyllodes Exposed to Different Light Treatments

Stage of phyllode development[++]	Light treatment[+++]	Total soluble protein		RuBPcase[+]	
		mg g^{-1}	mg dm^{-2}	mg g^{-1}	mg dm^{-2}
Fully developed	HH	4.86a[++++]	16.21a	1.22a	4.42a
	HL	5.12a	15.36a	0.87a	4.10a
Partially developed	HH	5.70a	19.05a	1.02a	4.36a
	HL	5.96a	18.49a	1.05a	3.53a

[+]Ribulose-1,5-bisphosphate carboxylase.

[++]Stage of development when the change in light level occurred.

[+++]See Table 15 for an explanation of light treatments.

[++++]Each value is a mean of five observations. Values in columns for a leaf development stage followed by the same letter are not significantly different at the 0.05 level of probability.

exposed to full sunlight and sun leaves become shaded. When koa seedlings were transferred from 73 percent shade to full sunlight, and from full sunlight to 73 percent shade, leaves and phyllodes readily adapted to the new light environments. Seedling terminals were not injured or defoliated, nor did solarization of chlorophyll within the leaves occur. Instead, leaves and phyllodes adapted physiologically and morphologically to both an increase and a decrease in light. Fully-developed leaves and phyllodes adapted only physiologically to the change in light, while partially-developed leaves and phyllodes also adapted morphologically.

Morphological Adaptation

Leaf morphology was greatly affected by changes in available light. If a seedling with phyllodes was shaded for 6 to 8 weeks, leaves instead of phyllodes began to develop at the terminals. A leaf is apparently better adapted to low light as it displays more than 3 times the absorbing surface as a phyllode (Chapter III). Leaflets also adjust to maintain an angle perpendicular to the sun. Phyllodes on the seedling when shading treatments were begun, persisted after shading. If seedlings were again exposed to full sunlight (maximum levels of at least 1200 μmol $m^{-2}s^{-1}$), new phyllodes developed instead of leaves.

The morphological adaptability of individual leaves and phyllodes depended upon their stage of development when shading was imposed or removed. Leaves and phyllodes that were fully-developed when the light level was increased or decreased did not adapt morphologically as evidenced by nonsignificant changes in SLWs (Table 15). In

contrast to the data for koa, the leaves of soybean (Glycine max var Ransom) adapted morphologically even when the change in light occurs after leaf expansion is complete (Bunce et al. 1977). When light is increased, soybean leaves become thicker in cross section and smaller in area. Conversely, when leaves are shaded, they become thinner in cross section and larger in area.

Leaves and phyllodes that were only partially-developed when the shading treatments were imposed or removed adapted morphologicaly as evidenced by significant changes in SLW (Table 15). Leaves and phyllodes that were exposed to higher light became thicker in cross section and surface area decreased. Leaves and phyllodes that were exposed to low light became thinner in cross section and larger in surface area. A greater surface area would allow greater light absorption, but a thinner cross section would result in lower mesophyll conductance to CO_2 because of a lower mesophyll surface area (Bunce et al. 1977, Nobel et al. 1975).

Physiological Adaptations

Both leaves and phyllodes, regardless of their stage of development, adapted physiologically to increased and decreased light. When light was decreased, the CER of fully-developed leaves and phyllodes changed in opposite directions. Phyllode CER at 1250 $\mu mol\ m^{-2}s^{-1}$ increased significantly, whereas leaf CER at the same PPFD decreased significantly. Soybean leaves subjected to a similar decrease in PPFD exhibited an increase in CER similar to that found for phyllodes (Bunce et al. 1977). The increase in CER of phyllodes may be accounted for by the significant increase in the amounts of chl

a, b, and total, that occurred after shading (Table 21). The increased amount of chlorophyll would enhance light energy absorption for CO_2 fixation (Boardman 1977). Chloroplast ultra structure also changes when leaves are shaded; grana thickness has been found to thus increase enhancing energy absorption (Skene 1974). The amount of chlorophyll in leaves did not increase after shading as it did in phyllodes. The ratio of chl a/b did not change for either leaves or phyllodes, probably because the proportion of red to blue wavelengths was not changed by the shading material. The amount of RuBPcase decreased in both leaves and phyllodes as a result of shading. However, only the decrease occurring in leaves was significant. This decrease in RuBPcase could account for the decrease of CER in leaves because leaves in the HL treatment had lower RuBPcase levels than even the leaves in the LL treatment. Leaves grown under low light, typically have less RuBPcase than those grown under high light (Boardman 1977). The TSP/chl ratio of both fully- and partially-developed leaves and phyllodes decreased only slightly with shading. The TSP/chl ratio of leaves and phyllodes were typical of ratios reported for sun and shade leaves, respectively (Boardman 1977).

When seedlings were transferred from the LL to LH treatment, the CER of fully- and partially-developed leaves stayed about the same for all measurement PPFD. Apparently, the effect of the decrease in chl a, b, and total was offset by the increase in TSP and RuBPcase. The increase in RuBPcase that occurred for koa leaves in high light has been noted for a number of other species (Bjorkman et al. 1972, Boardman 1977, Dale 1974). The ratio of TSP to chlorophyll for both

fully- and partially-developed leaves increased significantly at high light relative to that in shade. This increase reflects the increase of TSP and the decrease in chlorophyll that occurred when the light level was increased. Both fully- and partially-developed leaves in the LL treatment already had TSP/chl ratios typical of sun leaves (Boardman 1977).

CHAPTER VI

GENERAL SUMMARY AND CONCLUSIONS

Acacia koa is Hawaii's most valuable forest tree. It is considered a pioneering species because it becomes established rapidly after overstory removal if seeds are present in the soil. The two leaf forms of koa apparently allow it to gain and then maintain control of the site. The bipinnate juvenile leaves appear first. The leaves are long and wide compared to the phyllode. The compound nature of the leaf allows light to penetrate to the lower leaves. The leaflets are small and smooth, and adjust to maintain an angle perpendicular to the sun. As the seedlings grow and LAI increases, competition for light also increases. Koa apparently adapts by developing phyllodes. A canopy of steeply-inclined leaves is able to intercept more PPFD under field conditions than horizontal leaves. The development of phyllodes is apparently an adaption to reduced moisture availability (Farrell and Ashton 1978, Tunstall and Connor 1975). Phyllodes persist under conditions that result in the loss of leaves.

Although leaves and phyllodes differ markedly in leaf orientation, morphology, and anatomy, and in the levels of chlorophyll, TSP, and RuBPcase, they both had similar CER characteristics when determined on a leaf area basis. Mean maximum rates of photosynthesis for both leaf forms were about 24 mg CO_2 $dm^{-2}h^{-1}$. Light saturation and light compensation for both leaf forms occurred at 1200 and 25 µmol $m^{-2}s^{-1}$, respectively. The CO_2 compensation concentration was about 55 ppm for both leaves and

phyllodes, indicating that both leaf forms fix CO_2 via the C_3-pathway. The transpiration and leaf conductance rates, if determined for leaves orientated horizontally and phyllodes vertically, were also similar for both leaf forms.

Shading treatments imposed during growth greatly reduced koa seedling growth and development. Seedlings grown under the high light were the tallest and had the largest stem diameter and total dry weight. All measured growth parameters decreased as the light level was decreased. Although light saturation of CER of a single leaf occurs at about 1200 μmol $m^{-2}s^{-1}$, total CO_2 assimilation in a full canopy would be expected to increase with increasing light. As the seedlings grew and developed under the different levels of shade, roots as a percentage of the total dry weight remained a fairly constant 18 percent. Initially, leaves made up more than 50 percent of the total dry weight. The percentage of leaf dry weight decreased with time, while the percentage of stem dry weight increased. Phyllodes developed only on seedlings exposed to the highest light levels. The data indicated that koa seedlings can survive and grow only at light levels equal to or greater than 25 percent of full sunlight. The vigor of koa seedlings grown at less than 25 percent full sunlight declined with time and it appeared that they would eventually die. This minimum light requirement accounts for the scarcity of natural koa reproduction in an undisturbed koa forest.

Koa leaves and phyllodes readily adapt to changes in available light. If light levels are increased, both leaves and phyllodes

develop characteristics of sun leaves. Conversely, in low light, both leaf forms develop characteristics of shade leaves. Fully-developed leaves and phyllodes adapt only physiologically to changes in light level. Partially-developed leaves and phyllodes adapt both physiologically and anatomically to changes in light level.

Seedlings with phyllodes left under shade for 6 to 8 weeks began to develop leaves at the terminals. Seedlings again produced phyllodes when placed in full sunlight.

APPENDIX A

Table 25

Solar Radiation, Cumulative Rainfall, and Temperatures at Waimanalo, Hawaii for the Period October 1, 1980 to April 28, 1981

Date period	Solar radiation	Cumulative rainfall	Temperature	
			Maximum	Minimum
	Cal $cm^{-2}day^{-1}$	mm	- - - C - - -	
10/1 - 10/14/80	149	10.7	29.1	21.8
10/15 - 10/28/80	97	11.9	28.2	22.4
10/29 - 11/11/80	218	15.5	28.1	20.8
11/12 - 11/25/80	169	7.4	27.7	21.4
11/26 - 12/9/80	250	61.5	27.4	18.3
12/10 - 12/23/81	184	228.4	26.7	19.1
12/24/80 - 1/6/81	242	68.3	27.4	20.0
1/7 - 1/20/81	266	61.7	26.7	17.3
1/21 - 2/3/81	301	11.7	27.0	19.0
2/4 - 2/17/81	313	36.6	26.5	17.9
2/18 - 3/3/81	201	23.4	26.1	20.5
3/4 - 3/17/81	371	15.0	25.7	19.3
3/18 - 3/31/81	387	10.4	26.0	18.9
4/1 - 4/14/81	419	55.4	26.5	19.9
4/15 - 4/28/81	463	15.5	27.0	20.8

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